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Torymidae (Hymenoptera: Chalcidoidea) Associated with Bees (Apoidea), with a List of Chalcidoid Bee Parasitoids

E. E. Grissell

Systematic Entomology Laboratory, PSI, Agricultural Research Service,
U. S. Department of Agriculture, c/o National Museum of Natural History, Smithsonian Institution,
P.O. Box 37012, MRC 168, Washington, D. C. 20013-7012

Abstract.—Thirty-one species of Torymidae (Hymenoptera: Chalcidoidea) are associated with bees. In this review each is keyed and discussed, and geographic ranges and hosts are given. Most species are illustrated. Torymids represent about one-fourth of the 135 species of Chalcidoidea associated with bees. Two summary lists are presented for all chalcidoids, including Torymidae, and the 216 bee species with which they are associated. One is arranged as a bee/parasitoid list and the other as a parasitoid/bee list.

Considering that 22,000 species of Chalcidoidea (Noyes 2003) and 16,000–17,000 bee species (Michener 2000) have been described, the number of chalcidoids reported associated with bees is surprisingly small. At most 135 different chalcidoids have been reared from, or associated with, 216 bee species (see Appendix, derived from Noyes 2003). Of these, the families Torymidae and Leucospidae have the highest percentage of the bee parasitoids (each 22–23%), followed closely by Pteromalidae (18%). The other families associated with bees are: Encyrtidae (13%), Eulophidae (13%), Chalcididae (5%), Eurytomidae (5%), Eupelmidae (3%), Mymaridae (0.6%), and Perilampidae (0.6%) (Appendix: based on Noyes 2003).

Although Torymidae and Leucospidae have the highest number of bee parasitoids among Chalcidoidea, this figure is somewhat misleading. Of approximately 1,000 torymid species, only 31 are known (or suspected) to attack bees (Grissell 1995, 2000, 2005; Noyes 2003), so a predilection for bee hosts is not especially pronounced in the family. The host range of this family is extremely broad, but nearly 80% of the known hosts are shared equally between the Hymenoptera and Diptera, most of which are gall-forming cynipids and cecidomyiids (Grissell 1995). Conversely, the entire family Leucospidae, consisting of 135 species, has been presumed to parasitize aculeate Hymenoptera—solitary bees, and less frequently, solitary wasps. In reality, however, hosts are known only for about 30 leucospid species (Bouček 1974, Noyes 2003), so the true relationship of the family to bees is largely unknown. Recently a species of leucospid was reported as an ectoparasitoid of an ichneumonid attacking a cerambycid in limbs of apricot in Iran (Hesami et al. 2005). This finding casts doubt on our concept of host specificity in Leucospidae.

In this paper I present a summary of torymid species reported to attack bees, including a review of published information for each species and a key. I also include a world bee/chalcidoid and chalcidoid/bee list for all Chalcidoidea reportedly associated with bees (Appendix).

As with many chalcidoid records, the true host is not always indicated by the host record given (Noyes 1994). Many bee host records are simply nest rearings and may have been contaminated by other true parasitoids, cleptoparasitoids, inquilines, and simple space usurpers of all sorts, many not even hymenopteran. Similarly, a mud wasp's nest may be usurped by a nesting bee, thus causing confusion as to the true host (Rust 1974). Bee nests, as well as almost any other ecological niche, offer complex arrays of hosts, many of which are not even suspected at the time of rearing. For example, *Glyphomerus stigma* (Fabricius) was reported from *Melitoma taurea* (Say) (Apidae), but this is likely to be an error because all other records for species of *Glyphomerus* are gall-forming cynipids or rarely eurytomids (Grissell 1995). With respect to bee parasitoids, therefore, all records should be considered tentative until established by dissection and observation. Within the Torymidae listed in this paper, I point out that several are likely not to be true bee parasitoids. In those few cases where the biologies of torymids are known they are generally solitary, idiobiotic larval ectoparasitoids, but in several genera (e.g., *Monodontomerus*, *Microdontomerus*) larvae are known to be gregarious (Grissell 2000, 2005).

In examining host records presented in the Appendix several reviewers suggested that it might be informative to summarize parasitoid data with respect to bee biology as there appeared to be a bias towards twig and cavity nesting bees, with ground-nesters being under-represented. I solicited the input of two recognized bee authorities: Frank Parker, who specializes in twig-nesters, and Jerry Rozen, who specializes in ground-nesters, and both agreed that the data suggested cavity nesters were the predominant host representatives. These are primarily twig nesters, bees that nest in pre-existing crevices or cavities, and bees that re-use old bee nests. Some of these nests may be external, for example resin nests attached to objects such as twigs and rocks. According to Rozen most of the records are indicative of shallow nesting bees, and he suggested that ground nesting bees in general would be less likely to harbour parasitoids because they might have a more difficult time entering nests and crawling down the "... long, main tunnels" to find their host. He also pointed out that old bee nests and shallow cavities are frequently re-used several times, thus encouraging the build-up of large parasitoid populations. Parker suggested that twig-nesting bees are more likely to be sampled because they readily come to artificial traps set out by the collector. They are also easier to extricate and study in these nests. Conversely, ground nesting bees must be actively hunted by the collector, are less easily found, and require painstaking excavation to reveal nest details.

In general, then, records summarized in the Appendix indicate that host data are biased towards parasitoids attacking cavity nesting bees and that multiple causes contribute to this bias. Whatever cursory glimpses the bee/parasitoid host list may reveal, and considering the numerical size of the chalcidoid and apoid groups, it appears that much remains to be discovered. Within existing literature, relatively little is devoted to parasitization and then primarily only to a few solitary bee species (e.g., the alfalfa leafcutting bee, Stolbov et al. 1986), whereas with few exceptions (e.g., Zerova and Romasenko 1986) there is scarcely any comprehensive literature pertaining to solitary bee parasitoids.

METHODS

In the following discussions host names are given without authors. Complete authors' names may be found in the Appendix. Within discussions, hosts are listed alphabetically by family, but in the host listing all hosts are alphabetic regardless of family.

KEY TO TORYMIDAE ASSOCIATED WITH SOLITARY BEES

1 Anterior edge of metapleuron straight, not projecting forward as lobe into mesepimeron (Fig. 2) 4

— Anterior edge of metapleuron (usually its upper half) projecting forward as lobe into mesepimeron (Fig. 1), which is subdivided into upper and lower sections, lower section delimited by anterior groove ..... *Torymus* Dalman 2

2 Hind coxa dorsally covered with short setae (Fig. 3), coarsely reticulate; propodeum areolate-rugose, heavily carinate (Fig. 5); frenal area less than 1/5 length of scutellum (Fig. 7) 3

— Hind coxa dorsally bare (a few long setae may be present; Fig. 4), smooth and polished; propodeum essentially smooth (Fig. 6); frenal area 1/3 to almost 1/2 length of scutellum (Fig. 8) (Palearctic, Australasian [?introduced]) ..... *Torymus armatus* Boheman

3(2) Head dorsum, mesosoma, and hind coxa coppery with greenish tints; at least part of hind femur orange, concolorus with tibia (Palearctic) ... *Torymus cupreus* (Spinola)

— Head dorsum, mesosoma, and hind coxa metallic green or blue; entire hind femur metallic green or blue, contrasting with orange tibia (Nearctic) ..... *Torymus zabriskii* (Cresson)

4(1) Fore wing with marginal and stigmal veins conspicuously thickened relative to submarginal vein, postmarginal vein not projecting beyond tip of stigmal vein (Figs 9, 12, 13), and with marginal vein slightly removed from margin of wing (Fig. 13; may be somewhat difficult to see); malar distance longer than intermalar distance (Figs 14, 15); mandibles reduced, scarcely visible, tips not meeting medially when closed, apically without teeth ..... *Echthrodape* Burks 5

— Fore wing with marginal and stigmal veins not conspicuously thickened relative to submarginal vein, with postmarginal vein longer than stigmal vein (Fig. 10), and with marginal vein at edge of wing margin; malar distance subequal to or shorter than intermalar distance (Fig. 11); mandibles visible, tips meeting medially when closed, apically with teeth 6

5(4) Postmarginal vein developed, longer than stigmal vein, which is slender and petiolate (Fig. 12); genae straight, not concave (Fig. 14) [Papua New Guinea, Australia] ..... *Echthrodape papuana* Bouček

— Postmarginal vein reduced, subequal to stigmal vein, which is thick and sessile (Fig. 13); genae concave (Fig. 15) [Kenya] ..... *Echthrodape africana* Burks

6(4) Occipital carina absent (Fig. 16), weakly or questionably developed, or if apparent, then medially arched and midway between hind ocelli and occipital foramen and not reaching hypostomal carina (Fig. 17) (head usually vertical with dorsoposterior aspect slightly concave and the carina, if present, easily seen); hind femur slender, apicoventrally either without tooth (Fig. 34), angulate, or vaguely serrate; metasomal terga with or without apicomedian emarginations, often weakly sclerotized 26

— Occipital carina well developed, dorsal margin not greatly arched but nearly horizontal (Fig. 18), closer to occipital foramen than to hind ocelli and reaching hypostomal carina (head usually tilted forward with dorsoposterior aspect conspicuously concave and occipital carina easily seen, but head must be removed to see hypostomal carina); hind femur apicoventrally with abrupt tooth (Figs 35, 37, 38), or greatly swollen and angulate (Fig. 36); metasomal terga heavily sclerotized, without apicomedian emarginations [Holarctic, Neotropical, Oriental] ..... *Monodontomerus* Westwood 7

7(6) First 2 flagellar segments reduced in length, ring-like (Fig. 19); hind femur swollen with distal subapical angle but without distinct tooth (Fig. 36) [Nearctic] ..... *Monodontomerus thorpi* Grissell

— At most, first flagellar segment reduced in length (Fig. 20); hind femur relatively narrow with distinct subapical tooth (Figs 37, 38) 8

8(7) Female, face transverse, intermalar distance 3.5 to 5× length of malar distance; male, face grotesquely modified, entirely sunken medially (as if entirely consisting of scrobal basin) (Fig. 22), with sharp edge mesad of eye (Fig. 21) [Palearctic, Nearctic (introduced)] ..... *Monodontomerus osmiae* Kamijo

— Both sexes, face at most slightly transverse, intermalar distance from 1 to 3× length of malar distance; male with face not medially sunken, scrobal basin normal, though areas on either side of scrobe may be slightly depressed 9

9(8) Clypeus greatly elongate (Figs 23, 24) [Palearctic] .. *Monodontomerus anthidiorum* Lucas

— Clypeus either barely reaching to or beyond line drawn across lateral corners of oral fossa (Figs 25–28) 10

10(9) Upper mesepimeral area with anterior half reticulately sculptured and anterodorsal corner diagonally striate extending nearly to transepimeral sulcus (Fig. 53) 11

— Upper mesepimeral area nearly entirely polished with striae scarcely extending half way to transepimeral sulcus (Figs 54, 55) 12

11(10) Discal setae of fore wing not extending into basal area (as in Fig. 31); female with ovipositor sheaths shorter than metasoma; male with clypeus recessed (not extending beyond line drawn across lateral corners of oral fossa), malar sulcus absent or obscure, malar distance subequal to intermalar distance; scape with ventral surface slightly keeled vertically (i.e., not flat), no pores visible [Palearctic] ..... *Monodontomerus laticornis* Grissell and Zerova

— Discal setae of fore wing extending into basal area (as in Fig. 29); female with ovipositor sheaths as long as or longer than entire body; male with clypeus extending beyond line drawn across lateral corners of oral fossa, malar sulcus present; malar distance about 1.5× intermalar distance; scape with ventral surface flat, covered with pores visible at 100× [Nearctic] ..... *Monodontomerus clementi* Grissell

12(10) Metasomal tergum 2 dorsally with reticulate to strigate sculpture in distal half ... 13

— Metasomal tergum 2 dorsally smooth, polished in distal half 14

13(12) Distal portion of postmarginal vein equal in length to proximal portion (as in Fig. 30); rim of scutellum apically widened, somewhat projecting; females, metasomal tergum 6 acute in profile (as in Fig. 32); male, fore leg unmodified (i.e., normal) (as in Fig. 39), tibia equal in length to femur and not ventrobasally concave, tarsomeres elongate (claw length equal to or shorter than tarsomere 4) [Nearctic] ..... *Monodontomerus dianthidii* Gahan

— Distal portion of postmarginal vein 0.33× length of proximal portion (as in Fig. 31); rim of scutellum apically even in width, not projecting; female, metasomal tergum 6obtuse in profile (as in Fig. 33); male, fore leg modified (Fig. 40), tibia shorter in length than femur and ventrobasally concave, tarsomeres shortened (claw length equal to tarsomeres 3 and 4) [Nearctic] ..... *Monodontomerus brevicrus* Grissell

14(12) Malar sulcus absent (Fig. 28), or if weakly apparent, greatly curved backward from lower margin of eye then curving downward to join edge of malar opening (Fig. 27); lower face protuberant in profile (Fig. 28) [Nearctic] ..... *Monodontomerus bakeri* Gahan

— Malar sulcus well developed, straight (Figs 25–26), or slightly curved from lower margin of eye to lateral edge of malar opening; lower face flat (not bulging) in profile (Fig. 26) 15

15(14) Frenal area medially highly polished, appearing glabrous, faint coriaceous sculpture may be seen with difficulty at some angles of view (questionable species will run through either couplet of key) 16

— Frenal area medially sculptured, may be uniformly similar overall or relatively less prominent than laterally, never glabrous, sculpture easily visible at any angle of view (questionable species will run through either couplet) 19

16(15) Costal cell above with apical setal row incomplete, confined to distal 1/2 or less of cell (as in Fig. 31); female, metasomal tergum 6 strongly concave in profile (as in Fig. 32) [Nearctic] . . . . . *Monodontomerus torchioi* Grissell (most specimens)

— Costal cell above with apical setal row complete (as in Fig. 29); female, metasomal tergum 6 weakly concave in profile (as in Fig. 33) 17

17(16) Frenal area apicomedially intruding into rim, punctures of rim reduced in size at point of intrusion (Fig. 42); stigma and uncus relatively short, postmarginal vein with proximal and distal section subequal in length (Fig. 30) [Holarctic] . . . . . *Monodontomerus aeneus* (Fonscolombe)

— Frenal area with apical rim not interrupted posteriorly at median margin, punctures of rim as large or larger at apex as on sides (as in Fig. 41); stigma and uncus elongated, postmarginal vein with proximal section longer than distal (as in Fig. 31) 18

18(17) Female ovipositor sheaths swelling distally (i.e., not parallel-sided); male hind femur broad, widening apically, about 2.5× as long as wide (Fig. 38) [Palearctic] . . . . . *Monodontomerus rugulosus* Thomson

— Female ovipositor sheaths same width throughout (i.e., parallel-sided); male hind femur narrow, dorsal and ventral margins essentially parallel (Fig. 37), about 3.5× as long as wide [Neotropical] . . . . . *Monodontomerus argentinus* Brèthes

19(15) Costal cell above with apical setal row complete (Fig. 29) 20

— Costal cell above with apical setal row incomplete, confined to distal 1/3 to 1/2 of cell (Fig. 31) or appearing absent (2 or 3 setae may be present at apex as in Figs 43, 44) . . . 22

20(19) Scape about 4× longer than wide, greater in length (about 1.3×) than distance from venter of torulus to apical margin of clypeus [Nearctic, Neotropical] . . . . . *Monodontomerus mexicanus* Gahan

— Scape about 3× longer than wide, subequal in length to distance from venter of torulus to apical margin of clypeus 21

21(19) Stigma rectangular, proximally elongated towards base of wing (Figs 51, 52); postmarginal vein with distal length less than proximal length (Figs 51, 52); male face with depression laterad of scrobal basin [Nearctic] . . . . . *Monodontomerus acrostigmus* Grissell

— Stigma squarish, neither stigma nor proximal angle elongated (as in Figs 10, 44); postmarginal vein with distal length subequal to basal length (as in Fig. 44); male face convex laterad of scrobal basin [Holarctic] . . . . . *Monodontomerus obscurus* Westwood

22(19) Admarginal setae reaching bases of marginal vein and parastigma (Fig. 43); intermalar distance subequal to 3× malar distance (Fig. 48); both mandibles with single apical tooth and small secondary tooth on dorsal margin (Fig. 48) [Nearctic] . . . . . *Monodontomerus mandibularis* Gahan

— Admarginal setae either not reaching base of marginal vein or apex of parastigma (Fig. 44); intermalar distance less than 2.5× malar distance (Fig. 47); both mandibles with 2 apical teeth, and small third tooth on dorsal margin (Figs 47) 23

23(22) Transepimeral sulcus incomplete (Figs 53, 55); upper anterior margin of costal cell with setal row in apical 1/4 to 1/3 (as in Fig. 31); male, scape in side view slightly curved in profile (Fig. 56), area beneath torulus flat, sculptured, and setose 24

— Transepimeral sulcus complete (Fig. 54), appearing as a sculptured groove; upper anterior margin of costal cell with 1 to 3 setae at apex (Figs 43, 44); male, scape in lateral view strongly C-shaped (Figs 57, 58), area beneath torulus slightly swollen, polished, and asetose 25

24(23) Frenal area medially with reticulate sculpture readily apparent, area may be shiny, but sculpture visible at any angle of view; male, ventral surface of scape without pores visible at 100× [Nearctic] . . . . . *Monodontomerus montivagus* Ashmead

— Frenal area medially with reticulate sculpture visible only at some angles of view and seen only with difficulty, area shiny and appearing polished; male, ventral surface of scape evenly covered with pores easily visible at 100× [a few atypical specimens run here, but most to couplet 16 based on the polished frenal area] [Nearctic] ..... *Monodontomerus torchioi* Grissell

25(23) Females, ovipositor subequal to metasoma (ca. 1–1.2×); scape orange to yellow without metallic infusion especially ventrally; male, scape greatly laterally compressed (ventral and dorsal surfaces essentially absent), outer surface flat, polished, asetose, and curving smoothly to inner surface without interruption (Fig. 57), no pores visible at 100× [Nearctic] ..... *Monodontomerus parkeri* Grissell

— Females, ovipositor obviously longer than metasoma (ca. 1.5–1.8×); scape with metallic green infusion at least ventrally (may be complete or confined to area just beneath pedicel); male, scape dorsoventrally compressed, curved, with dorsal and ventral surfaces parallel and delimited by right-angled edge (Fig. 58), ventral surface polished and covered with pores visible at 100× though difficult to see [Nearctic] ..... *Monodontomerus tepedinoi* Grissell

26(6) Marginal vein long, 3–7× length of postmarginal vein and at least 6× length of stigmal vein; occipital carina present, its lateral edges extending at least in line with *dorsum* of hypostomal foramen [Oriental] ..... *Pseudotorymus indicus* (Mani)

— Marginal vein short, 1–2.5× length of postmarginal vein and 2–5× length of stigmal vein (Figs 45, 46); occipital carina absent (Fig. 16) or, if present, its lateral edges not (or scarcely) extending in line with *venter* of occipital foramen (Fig. 17) 27

27(26) Occipital carina absent (Fig. 16) ..... *Microdontomerus* Crawford 28

— Occipital carina visible in dorsal view as finely polished line raised distinctly above surface sculpture (as in Fig. 17) [Palearctic] .... *Adontomerus* Nikol'skaya (*A. gregalis* (Steffan) and *A. nesterovi* Zerova)

28(27) Fore wing setation (Figs 45, 46) reduced; basal cell open behind, i.e., cubital vein basally at most with few isolated setae; basal vein at most with isolated setae; basal cell without distinct setal row paralleling submarginal vein 29

— Fore wing setation (as in Figs 29, 31) not reduced (except in admarginal area of some species): basal cell closed behind, i.e., cubital vein essentially completely setose to base of wing; basal vein with distinct setal row and basal cell with setal row paralleling nearly entire submarginal vein 30

29(28) Postmarginal vein (Fig. 46) about 0.75× as long as marginal vein; fore wing with admarginal area (Fig. 46) not well defined posteriorly by setal line, with admarginal setae nearly as uniform as central area of wing [Nearctic] .... *Microdontomerus enigma* Grissell

— Postmarginal vein (Fig. 45) about 0.5× as long as marginal vein; fore wing with admarginal area (Fig. 45) well-defined posteriorly by setal line, with few sparse setae not as uniform as central area of wing [Nearctic] .... *Microdontomerus parkeri* Grissell

30(28) Eye height nearly 3× malar distance (Fig. 49); distance between eyes less than eye height (Fig. 49) [Nearctic] ..... *Microdontomerus anthidii* (Ashmead)

— Eye height 2.5× or less than malar distance (Fig. 50); distance between eyes equal to eye height (Fig. 50) [Nearctic] ..... *Microdontomerus apianus* Grissell

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Adontomerus Nikol'skaya

Recognition.—*Adontomerus* is recognized by the straight anterior edge of the metapleuron (Fig. 2); the fore wing with marginal vein 1 to 2.5× the length of the postmarginal vein, 2 to 5× the length of the stigmal vein, and marginal + postmarginal veins equal to 0.2× the length of the wing; the occipital carina visible in dorsal view as a finely polished line raised distinctly above surface sculpture, medially arched

and midway between hind ocelli and occipital foramen (Fig. 17); and the hind femur ventrally without a tooth (as in Fig. 34).

Number of Species.—8.

Number Associated with Bees.—2.

Distribution.—Species of this genus are reported in the Palearctic Region including the former Soviet Union, Bulgaria, former Yugoslavia, Hungary, Italy, Sardinia, Spain, Jordan, and Algeria.

Hosts of Genus.—Species of *Adontomerus* have been reared from cocoons of Lasiocampidae (Lepidoptera), galls of Cynipidae (Hymenoptera), and cocoons of Megachilidae (Hymenoptera). In the National Museum of Natural History, Washington, DC, there are specimens reared from weevils in seed heads of Asteraceae.

Discussion.—Records for the species listed below have been cited in the literature under the genus *Mellitotorymus*, which was synonymized with *Adontomerus* by Grissell (1995).

Adontomerus gregalis (Steffan)

Distribution.—PALEARCTIC: Reported only from Sardinia (Steffan 1964).

Host.—Reared from *Pseudoanthidium* (reported as *Anthidium*) *lituratum* (Megachilidae).

Discussion.—I believe that this species and *Adontomerus nesterovi* are synonyms, but I have not seen material of the latter to confirm this. Both share essentially similar descriptions as well as the same host. I treat them separately here to retain the known data, but there is no way to distinguish the species as far as I can tell.

Adontomerus nesterovi Zerova

Distribution.—PALEARCTIC: Reported from Turkmenistan (Zerova and Romasenko 1986).

Host.—Reared from cocoons of *Pseudoanthidium* (as *Paraanthidiellum*) *lituratum* (Megachilidae).

Discussion.—Zerova and Romasenko (1986) keyed and figured this species in a paper on the parasitoids of megachilid bees in the former Soviet Union.

Echthrodape Burks

Recognition.—*Echthrodape* is recognized by the straight anterior edge of the metapleuron (as in Fig. 2) and by the relatively short wing venation and the thickened marginal vein (Figs 9, 12, 13), with the postmarginal vein some distance from the distal edge of the wing (Fig. 9). Additional characters that help in recognition are the toothed hind femur (as in Fig. 38), the developed occipital carina that lies midway between the hind ocelli and occipital foramen, and the reduced mouth opening (Figs 14, 15, indicated, in part, by the long malar distance) with reduced mandibles (scarcely visible and obscured by other mouth parts).

Number of Species.—2.

Number Associated with Bees.—2.

Distribution.—The genus is found in the Afrotropical Region in Kenya, and in the Australasian Region from Papua New Guinea.

Host.—Hosts for both species belong to the genus *Braunsapis* (Apidae).

Discussion.—The species of this genus are uncommonly encountered and are presently the only indigenous torymid bee parasitoids known from sub-saharan Africa and Australasia. The lack of records for these areas is probably the result of a paucity of collecting and rearing both bees and parasitoids.

Echthrodape africana Burks

Distribution.—AFROTROPICAL: Reported from Kenya (Burks 1969).

Host.—Reared from nests of *Braunsapis* (as *Allodapula*) (Apidae) as reported by Burks (1969) and expounded upon by Michener (1969) who reported the following host records: *Braunsapis simplicipes*, *B. rolini*, and *B. rufipes*.

Biology.—Larvae of *E. africana* are external feeders on pupae of *Braunsapis* (Michener 1969). One parasitoid was seen per host. The bee is a progressive feeder which uses burrows in the pith of dead *Lantana* stems. It moves its larvae and pupae about and does not distinguish between its own progeny and those of *E. africana*.

Morphology.—Michener (1969) illustrated and described the peculiar larva of this species as well as the pupa.

Discussion.—The two known species are relatively easily identified based on the distinctive heads (Figs 14, 15) and wing veins (Figs 12, 13) as well as their disjunct distributions.

Echthrodape papuana Bouček

Distribution.—AUSTRALASIAN: Known from Papua New Guinea (Bouček 1988) and Australia (R. Matthews, per. comm.).

Host.—Reared from cells of *Braunsapis unicolor* (Apidae) nesting in bamboo internodes (R. Matthews, per. comm.).

Discussion.—A voucher specimen for the Australian record was kindly placed in the U. S. National Museum collection by Robert Matthews.

Microdontomerus Crawford

Recognition.—Microdontomerus is recognized by the straight anterior edge of the metapleuron (as in Fig. 2), the simple hind femur (as in Fig. 34), the absence of an occipital carina (Fig. 16), and the marginal vein short, 1 to 2.5× the length of the postmarginal vein and 2 to 5× the length of the stigmal vein (Figs 45, 46).

Number of Species.—22.

Number Associated with Bees.—4.

Distribution.—This genus is transcontinental in the Nearctic, but limited in other regions of the world. In the Palearctic it is found in Spain, Italy, Algeria, and Libya, and in the Afrotropical Region it is found in Senegal. [The genus was reported in India (see Farooqi 1986, David et al. 1990), but this is probably a misidentification resulting from the confusion in names that existed at the time.]

Hosts.—Species are reported from megachilid bees and cynipid gall-formers (Hymenoptera), tephritids (Diptera), buprestid eggs and curculionids (Coleoptera), mantid eggs (Mantodea), and coleophorids, gelichiids, lasiocampids, and tortricids (Lepidoptera). At least one Nearctic species attacks saturniid eggs (Lepidoptera). Species have also been documented as facultative hyperparasitoids of braconids (Hymenoptera) (Grissell 2005).

Microdontomerus anthidii (Ashmead)

Distribution.—NEARCTIC: This species has been collected in southern California, USA.

Host.—Reared from *Dianthidium pudicum consimile* (as *Anthidium consimile*) (Megachilidae).

Discussion.—Microdontomerus anthidii, *M. enigma*, and *M. parkeri* are difficult to distinguish. Generally *M. anthidii* is smaller (2.3 mm or less) with a shorter ovipositor (less than 1.2× hind tibia), whereas *M. parkeri* is larger (up to 3.0 mm) with a longer ovipositor (more than 2× hind tibia). *Microdontomerus enigma* is about the size of *M. anthidii*, but with the longer ovipositor of *M. parkeri*. *Microdontomerus anthidii* is fairly easily separated from the other two, however, based on discrete morphological differences in the fore wing: *M. anthidii* has a complete setal row along the upper anterior margin of the costal cell (absent in the other two species) and the basal cell is closed (open in the other two species). It appears that while all three species attack megachilid bees, *M. anthidii* is usually associated with species of the tribe Anthidiini that create nests of resin and sand grains, whereas *M. parkeri* and *M. enigma* are associated with Osminiini and Megachilini that make stem nests.

Microdontomerus apianus Grissell

Distribution.—NEARCTIC: Known from California, USA.

Host.—Reared from *Megachile montivaga* (Megachilidae).

Discussion.—In addition to characters given in the key, this species differs from *M. anthidii* in having the intermalar distance about 1.7× the malar distance (about 2.5× in *M. anthidii*), and in having the ovipositor sheaths subequal to the body length and 2.0–3.0× as long as the hind tibia (in *M. anthidii* ovipositor sheaths subequal to metasoma and usually less than 1.5× as long as hind tibia).

Microdontomerus enigma Grissell

Distribution.—NEARCTIC: Known only from one locality in Nevada, USA.

Hosts.—Reared from *Hoplitis bullifacies* (Megachilidae).

Discussion.—This species is phenotypically nearly identical to *M. parkeri*. Characters to separate the two are given in the key. Somewhat more difficult to assess is that in *M. enigma* the longest diameter of the lateral ocellus is less than the ocellocular distance, whereas it is subequal to or greater than the distance in *M. parkeri*.

Microdontomerus parkeri Grissell

Distribution.—NEARCTIC: Widespread in the western and southwestern United States.

Hosts.—Reared from Megachilidae: *Ashmeadiella bigeloviae*, *Ashmeadiella cubiceps*, *Ashmeadiella gillettei*, *Ashmeadiella rufipes*, *Hoplitis bullifacies*, *Hoplitis palmarum*, *Megachile brevis*, and *Osmia marginata*.

Biology.—*Microdontomerus parkeri* is a gregarious parasitoid within individual bee cells. The number of individuals ranged from 2 to 33 per cell, with an average of about 8–9. For these rearings the total number of *M. parkeri* specimens was 229 females and 125 males for a sex ratio of 1.8 to 1. Ten of these rearings contained no males (Grissell 2005).

Discussion.—This species has also been reared from *Ancistrocerus* sp. and *Leptochilus* sp. (Vespidae: Eumeninae). It is the most common and widespread species of *Microdontomerus* attacking bees.

Monodontomerus Westwood

Recognition.—*Monodontomerus* is recognized by the straight anterior edge of the metapleuron (as in Fig. 2), the presence of a frenal line on the scutellum (as in Fig. 8), the hind femur with a single, apicoventral tooth (Figs 35, 37; though in one species this tooth is poorly defined, Fig. 36), and by the well developed occipital carina which is nearly horizontal on its dorsal margin and closer to the occipital foramen than to the hind ocelli (Fig. 18).

Number of Species.—32.

Number Associated with Bees.—19.

Distribution.—The species of this genus are widespread throughout the Holarctic, and somewhat less common in the Neotropical (Cuba, Mexico, Colombia, Argentina) and Oriental (Sri Lanka, India, Pakistan) regions.

Hosts.—Numerous hosts are known for this genus including families in Diptera, Hymenoptera, and Lepidoptera. The primary hosts are solitary aculeate bees and wasps, sawflies, and moths (including their tachinid and ichneumonid parasitoids). An authentic record of *Monodontomerus* (undetermined species) attacking social vespids (*Mischocyttarus*; Litte 1979) in Arizona occurs in the literature, but voucher specimens are now lost (Litte, *in litt.*). Unfortunately, some species of *Monodontomerus* are extremely difficult to tell apart and as a consequence there have been many misidentifications resulting in incorrect host records for some species. For example, *Monodontomerus aereus* Walker has been reported from *Megachile muraria* (now = *M. parietina*)(Constantineanu et al. 1956), but this would not be considered a host based on the majority of records, which are from Lepidoptera (Grissell 2000, Noyes 2003). *Monodontomerus vicicellae* (Walker), a common parasitoid of larval

Lepidoptera and sawflies, was reported to be reared from an ichneumonid parasitoid in the nest of *Megachile "ramulorum* Rond." (Rondani 1877), which is a *nomem nudum*. There are no other records from bees for this species and the host record is considered to be incorrect. Similarly, *Monodontomerus minor* (Ratzeberg), also a parasitoid of Lepidoptera and sawflies, has been reported from several bees, but while these records appear in lists (e.g., Herting 1977) they apparently have no basis in the primary literature.

Discussion.—In the following section, summary data are documented in Grissell (2000) unless otherwise specified. Identification is often more easily based on male characters. Although females predominate in reared series, species have gregarious larvae and some males are almost always present.

Monodontomerus acrostigmus Grissell

Distribution.—NEARCTIC: Eastern Texas, USA.

Hosts.—Reared from pupa of *Megachile* sp. (Megachilidae) in a "mud-dauber nest".

Discussion.—*Monodontomerus acrostigmus* is similar in appearance to *M. obscurus*, but differs from it (and all other known species) by having the stigma posteriorly appendiculate (Figs 51, 52). In addition, it differs from *M. obscurus* by having the distal portion of the postmarginal vein one half or less than the proximal portion (subequal in *M. obscurus*) and in males, which have the face lateral to the scrobal basin distinctly depressed (not depressed in *M. obscurus*).

Monodontomerus aeneus (Fabricius)

Distribution.—NEARCTIC: Widespread throughout the northern United States and southern Canada. PALEARCTIC: Reportedly widespread in western Europe (Nikol'skaya and Zerova 1978) and often confused with *M. obscurus*, which has the same distribution and general host range.

Hosts.—There are a great number of hosts listed for this species (as *obsoletus*) in the Old World (see Grissell 1995). Only bee hosts are listed here because these are certainly correct whereas all other hosts are suspect. Old World: *Anthophora retusa*, *Ceratina callosa* (Apidae); *Anthidium florentinum*, *Hoplitis* (as *Osmia*) *adunca*, *Megachile parietina* (as *Chalicodoma muraria*) (and *Stelis nasuta*, a cleptoparasite of this host), *Megachile apicalis*, *Megachile centuncularis*, *Megachile* (as *Chalicodoma*) *sicula*, *Osmia* (as *Metallinella*) *brevicornis*, *Osmia coerulescens*, *Osmia rufa cornigera*, *Osmia cornuta*, *Osmia emarginata*, *Osmia fulviventris*, *Osmia latreillei*, *Osmia rufa*, *Osmia submicans*, *Osmia tricornis* (all Megachilidae). New World: Verifiable records for this species include *Megachile concinna*, *Megachile rotundata*, and *Osmia nigrifrons* (Megachilidae).

Biology.—Newport (1849, 1852, 1853) provided information and illustrations of the larvae, their digestive tract, and feeding habits. Johansen and Eves (1966) and Eves (1970) (and possibly Hobbs and Krunic 1971) published biological information on this species (as *obscurus*, reidentified by me, based upon Eves' specimens) as a parasitoid of *Megachile rotundata*. Females oviposited through the leaf-lined cell and/or cocoon of the host. Between 3 and 51 eggs were laid externally on the host. An average of 10 survived in one study (Johansen and Eves 1966), but Bonelli and Campadelli (1990) gave an average of 24 (range = 10 to 51 adults for 15 bee cells). All immature stages of the host are vulnerable to attack but parasitization of early instars is rarely successful. Larvae are non-cannibalistic. The life cycle can be completed in about 20 days. Goodpasture (1975) detailed the mating behavior of *M. aeneus* (reported as *M. obscurus*, but subsequently confirmed as *M. aeneus* in Grissell 2000). Tepedino (1988a) demonstrated that 7–12% of females mated before emergence from the host cocoon. He also

showed (Tepedino 1988b) that females had an initial obligatory requirement for host cocoon and prepupal authenticity, but after 24 hours this would break down and females would oviposit into gelatin capsules holding bee prepupae or even agar replicates of bees. Females oviposited onto fresh host prepupae or prepupae that were up to 16 days old. Tepedino (1988c) showed that superparasitism occurs but that rates go down as resident parasitoids become older. In Spain, rates of parasitism for *M. aeneus* (reported as *M. obsoletus*) on *Osmia cornuta* (Megachilidae) varied from 0.5% (Bosch 1994b) to 73% (Bosch 1994a). According to Bosch (1993) 53–76% of managed bee cocoons were parasitized when paper straws containing bee cells were extracted from their nesting blocks, but cells left in grooved boards were left untouched. In the Nearctic this parasitoid (as *M. obscurus*) reportedly replaced the native species *M. montivagus* in the mid-1960's as the most important parasitoid of the alfalfa leafcutting bee in North America, but then was itself replaced by a pteromalid in the mid 1970's (Eves 1982). A paper on control of an unknown species of *Monodontomerus* in Utah by Brindley (1976) undoubtedly refers to this species.

Morphology.—Goodpasture illustrated the karyotype of *M. obsoletus* (1975, reported as *M. obscurus* but confirmed as *M. aeneus* by Grissell 2000). The chromosomes number 4 in males, 8 in females. Goodpasture (1975) illustrated male scapes, and Walther (1983) illustrated antennal sensillae of this species.

Discussion.—This species was introduced into the Nearctic in the 1930's (Johansen and Eves 1966), but it was misidentified as *M. obscurus*. Its correct identity as *M. obsoletus* was reported by Tepedino (1989) based upon my identification. The name has since been changed to *M. aeneus* by Graham (1992) who studied the type material of the species involved. Almost all previously published host records (e.g., Peck 1969) for *M. obscurus* are wrong and most should now refer to *M. aeneus*. Both *M. aeneus* and *M. obscurus* are common and widespread and are among the two most difficult species of the genus to distinguish from each other. This is disconcerting because they are economically important, have both been introduced into the New World along with the alfalfa leafcutter bee, and have been confused with each other since their introductions. Only the apparent absence of sculpture (though faint coriaceous sculpture may be apparent at some angles of view) on the median frenal area and the construction of the frenal apex offer reliable diagnostic information to separate these two species, but even this can be difficult to interpret on occasion. An additional character that may sometimes help to define these two taxa is found in the mesepimeron. In *M. aeneus* the entire mesepimeron is essentially smooth (polished) except for some slight reticulation (or carinae) above the ventral margin. In *M. obscurus* the ventral 1/5 of the mesepimeron below the transepimeral sulcus is reticulate and the anterior 1/3 is alutaceous to lightly reticulate.

Monodontomerus anthidiorum (Lucas)

Distribution.—PALEARCTIC: Found only in Algeria.

Host.—Reared from *Rhodanthidium sticticum* (Megachilidae).

Biology.—This species was reared from the larva of its host. According to Lucas (1849) the bee nested in empty snail shells (*Helix* spp). The larvae were gregarious with 40–50 specimens of *M. anthidiorum* found in each shell.

Discussion.—This species apparently has not been collected since its original description. In both sexes this is one of the most distinct species of the genus based on the elongated clypeus (Figs 23, 24).

Monodontomerus argentinus Brèthes.

Distribution.—NEOTROPICAL: Costa Rica, Panama, Colombia, and Argentina.

Hosts.—Reared from cells of *Eufriesea nigrescens* (as *Euplusia longipennis*) (Apidae) in Colombia. A species of *Megachile* (Megachilidae) also serves as host.

Biology.—Sakagami and Sturm (1965) reported that this species developed on the pupal stage.

Discussion.—*Monodontomerus argentinus* is similar to *M. mexicanus* especially in proportions of the head and antenna and in details of the wing. In both sexes of *M. argentinus* the median area of the frenum is highly polished, whereas in *M. mexicanus* the median frenal area is longitudinally sculptured similar to the lateral areas.

Monodontomerus bakeri Gahan

Distribution.—NEARCTIC: Colorado, Utah, Idaho, USA, and Alberta, Canada.

Hosts.—*Megachile pugnata*, *Megachile relativa*, *Megachile rotundata*, *Osmia coloradensis*, and *Osmia texana* (Megachilidae).

Discussion.—This species is relatively uncommon, but large numbers were trapped from *Megachile rotundata* blocks as a nuisance species at the USDA Bee Biology and Systematics Laboratory in Logan, Utah (pers. obs.). *Monodontomerus bakeri* is unique among species of the genus in two ways. The absence of a malar sulcus (Fig. 28), or its expression as a greatly curving, indefinite line (Fig. 27), is atypical compared to the straight, well-defined sulcus found in most other species (e.g., Fig. 26). Also, the bulging lower face (Fig. 27) is not found in any other species, all of which have the area essentially flat (as in Fig. 26).

Monodontomerus brevicrus Grissell

Distribution.—NEARCTIC: California, USA.

Hosts.—Reared from nests of *Osmia ribifloris* (Megachilidae).

Discussion.—*Monodontomerus brevicrus* resembles *M. dianthidii* in having metasomal tergum 2 dorsally sculptured, but it is separated as follows: Both sexes of *M. brevicrus* have the distal portion of the postmarginal vein about one-third the length of the proximal portion (Fig. 31) (about equal in *M. dianthidii*) and the rim of the scutellum apically even in width and not projecting (apically widened and somewhat projecting in *M. dianthidii*). In females of *M. brevicrus* metasomal tergum 6 is obtuse in profile (as in Fig. 33) (acute in *M. dianthidii*, as in Fig. 32) The males of *M. brevicrus* are unique among New World males in modifications found in the fore leg and in the sunken lower face. In males the fore leg is reduced (Fig. 40) with the tibia shorter in length than the femur and ventrobasally concave, and the tarsomeres shortened with the claw length equal to tarsomeres 3 and 4 (fore leg unmodified in other species, cf. Fig. 39).

Monodontomerus clementi Grissell

Distribution.—NEARCTIC: Wyoming and Colorado, USA.

Hosts.—*Dianthidium heterulkei* (Megachilidae) [also reared from the factitious host *Megachile rotundata* (Megachilidae) in the laboratory].

Biology.—Clement (1976) found this species feeding on prepupae in cocoons of *D. heterulkei*. Goodpasture (1975) described the mating behavior, which is identical to that of *Monodontomerus montivagus*.

Discussion.—*Monodontomerus clementi* and *M. laticornis* are similar in having the anterior half of the upper mesepimeral area reticulately sculptured and the anterodorsal corner with diagonal striations extending nearly to transepimeral sulcus (Fig. 53). They differ in the characters outlined in couplet 11 of the key.

Monodontomerus dianthidii Gahan.

Distribution.—NEARCTIC: Eastern California and southwestern Oregon, USA.

Hosts.—*Dianthidium* sp. (Megachilidae).

Biology.—Reared from resin nests.

Discussion.—*Monodontomerus dianthidii* is phenetically most similar to *M. brevicrus*

based upon the completely sculptured frenal area and metasomal tergum 2; the differences between these species are discussed in detail under *M. brevicrus* above.

Monodontomerus laticornis Grissell and Zerova

Distribution.—PALEARCTIC: Russia, Kazakhstan, Ukraine, and Moldavia.

Hosts.—Reared from *Megachile rotundata* (Megachilidae); *Megachile centuncularis* and *Anthidium florentinum* (Zerova and Stolbov 1986) (Megachilidae); *Anthidium septemspinosum* (Zerova and Seryogina (2002). [A report of *Apis mellifera* as host (documented in Noyes 2003) seems unlikely].

Biology.—This is a gregarious parasitoid within cocoons of the hosts.

Discussion.—Zerova and Romasenko (1986) key and figure this species in a paper on the parasitoids of megachilid bees in the Former Soviet Union. This species and *M. clementi* are similar in appearance, and characters to distinguish them are given under couplet 11 of the key. *Monodontomerus laticornis* is a Palearctic species and *M. clementi* a Nearctic one, so they should not be readily confused.

Monodontomerus mandibularis Gahan

Distribution.—NEARCTIC: Widespread throughout the eastern USA and Canada from Saskatchewan south to Louisiana.

Hosts.—*Anthophora abrupta*, *A. bomboides bomboides*, *Melitoma taurea* (Apidae); *Osmia cordata* (Megachilidae) (Rau 1947).

Biology.—Rau (1947) published some preliminary information on the life history of this species, which he concluded had one or two generations per year. He believed the wasp to be a primary, gregarious parasitoid of its host.

Discussion.—*Monodontomerus mandibularis* is morphologically similar to *M. montivagus* but differs in both sexes (and from all other *Monodontomerus* species) by the mandibles having a single large, ventral tooth and a smaller, subapical dorsal one (Fig. 48). Other species have two ventral teeth and a small subapical dorsal one (as in Fig. 47) or have the dorsal tooth so reduced as to be easily overlooked. The mandibles are not generally exposed, however, so that for practical purposes *M. mandibularis* is best distinguished from *M. montivagus* as follows: In females the intermalar distance is about 3× the malar distance (about 2× in *M. montivagus*; this is the result of the malar distance being relatively shorter in *M. mandibularis* and the face less produced ventrally below the eyes, cf. Figs 47, 48) and the posterior outline of metasomal tergum 6 is deeply concave (shallow in *M. montivagus*, cf. Figs 32, 33); in males the scape (Fig. 57) is laterally compressed and distinctly C-shaped in profile with dorsal and ventral arches asymmetrical (in *M. montivagus* the scape is dorsoventrally compressed and nearly symmetrically curved in profile, Fig. 56, sometimes greatly so).

Monodontomerus mexicanus Gahan

Distribution.—NEARCTIC/NEOTROPICAL: Spotty distribution in Arizona, north-central Mexico, and western Panama.

Hosts.—*Megachile peruviana* (Megachilidae) (Rau 1947); *Ancyloscelis apiformis* (as *armata*) (Torchio 1974) and *Anthophora marginata* (Apidae) (Herting 1977).

Discussion.—This species has also been reared from *Trypoxylon mexicanum* (Gahan 1941), *T. monteverde*, and *Passaloecus* (= *Polemistus*) *pusillus* (Rau 1947) (all Crabronidae). It has been seen walking on the surface of *Trypoxylon* mud nests and drilling with its ovipositor through the mud walls (Brockmann in *litt.*). It is similar to *M. argentinus* and is discussed under that species.

Monodontomerus montivagus Ashmead

Distribution.—NEARCTIC: Widespread throughout southern Canada and USA. NEOTROPICAL: Southern Mexico (Guerrero).

Hosts.—This species has been reared from the following bees. Apidae: *Anthophora abrupta, Anthophora bomboides bomboides, Anthophora bomboides neomexicana, Anthophora linsleyi, ?Anthophora occidentalis, ?Anthophora vallorum, Bombus morrisoni, ?Melissoides* sp., *Xylocopa tabaniformis orpifex*. Megachilidae: *Anthidium collectum, Anthidium emarginatum, Anthidium ?mormonum, Anthidium* nest, *Ashmeadiella californica, Dianthidium curvatum sayi, Dianthidium pudicum pudicum, Dianthidium pudicum consimile, Hoplitis anthocopoides* nest, *Megachile centuncularis, Megachile relativa, Megachile rotundata, Osmia* sp. cocoon (in *Trypoxylon politum* nest [Crabronidae]), *Osmia cordata, Osmia kincaidii, Osmia latisulcata, Osmia lignaria, Osmia ribifloris, Osmia sanrafaelae, Osmia texana, Stelis depressa*.

Biology.—This is a gregarious, external parasitoid of aculeate Hymenoptera. Although there are numerous references to this species in the literature (see Peck 1963), most of these are simply host records without biological data. A few papers cited by Peck are of interest and are cited below. Davidson (1893: 153) stated that females of *M. montivagus* deposited 10 to 20 eggs in each cell of *Xylocopa tabaniformis orpifex* and that some broods were all males while others were all females. Hicks (1926: 224) stated that *M. montivagus* was parasitic both on *Anthophora occidentalis* and its parasitoid *Oryttus miraudus*, thus acting as a primary and secondary parasitoid. Mickel (1928: 72–73) reared 415 specimens, of which 94% were females, from 21 cells of *Anthophora occidentalis*. He found no hyperparasitic relationship on the same bee host as reported by Hicks (1926). Linsley and MacSwain (1942: 409–411) also reported *montivagus* as both a primary and a hyperparasitoid on *Anthophora linsleyi* and its mutillid parasitoid *Photopsis auraria* (now = *Sphaeropthalma unicolor*). These authors discussed the courtship behavior of *montivagus* and stated that its larvae fed on the prepupal stage of the bee. They stated that only one cell (of 9) had mixed sexes of this parasitoid, the others being either female (average 26 per cell) or male (average 40 per cell). In later rearings, however, MacSwain (1958: 395) found mixes of males and females in each of four cells of *A. occidentalis*. The sex ratio (males:females) varied from 1 to 12 to 1 to 30. Rau (1922) found a ratio of 1 to 6. Goodpasture (1975) described and illustrated the courtship behavior of *M. montivagus*. It is apparent from the literature and from reared specimens that *M. montivagus* is parasitic on bees, wasps, and their nest associates. New and old nests of aculeate Hymenoptera are complex sites of diverse taxa, behaviorial types, and successional faunas. Therefore, our biological knowledge of *M. montivagus* is almost wholly inadequate.

Morphology.—Goodpasture (1975) described and illustrated the male scapes and the haploid karyotype. This species has 6 chromosomes in males, 12 in females.

Discussion.—Females of *M. montivagus* are morphologically similar to other species reared from bees (e.g., *M. parkeri, M. tepedinoi, M. torchioi, M. mandibularis*), but males differ notably in morphology of the scape. The differences between *M. montivagus* and the others mentioned are discussed under each of these species.

Monodontomerus obscurus Westwood

Distribution.—NEARCTIC: Widespread from coast to coast in the United States and southeastern Canada. [Undoubtedly introduced into the Nearctic along with its host the alfalfa leafcutting bee.] PALEARCTIC: Reportedly widespread in western Europe (Nikol'skaya and Zerova 1978) and probably often confused with *M. aeneus* which appears to be sympatric. The species is also reported from the oriental Region (India).

Hosts.—*Hoplitis* (as *Osmia*) *adunca, Megachile argentata, Megachile centuncularis, Megachile cephalotes, Megachile flavipes,*

Megachile lanata, *Megachile parietina* (as *Chalicodoma muraria*), *Megachile rotundata*, *M. willughbiella*, *Osmia cordata*, *Osmia cornifrons*, *Osmia latreillei*, *O. lignaria*, *Osmia ribfloris*, *Osmia rufa rufa*, *Osmia rufa cornigera*, *Osmia sanrafaelae*, (Megachilidae); *Anthophora plumipes*, *Xylocopa fenestrata* (Apidae).

Biology.—In Spain, *M. obscurus* is considered to be extremely destructive to the alfalfa leafcutting bee industry and chemical methods of control have been devised (Asensio 1982). Krunic and Radovic (1973) reported that *M. obscurus* can go through a number of generations without diapause and that diapause could be interrupted after keeping them for a time at 5° C.

Morphology.—Radu and Botoc (1968) illustrated female genitalia in detail. MacDonald and Krunic (1971) illustrated the somatic chromosomes for *M. obscurus*, which number 6 in males and 12 in females. (This differs from *M. aeneus* and thus strengthens the case for reproductive isolation between these two nearly identical species.) Baker et al. (1985) described and illustrated the last instar larva and pupa of this species (adult identity confirmed by examination of voucher specimens in North Carolina State University Insect Collection).

Discussion.—Zerova and Romasenko (1986) key and figure this species in a paper on the parasitoids of megachilid bees in the former Soviet Union. This species is similar to *M. aeneus* and is often reared from the same species of host in the same locality. I discuss the two species more fully under *M. aeneus*, above.

Monodontomerus osmiae Kamijo

Distribution.—PALEARCTIC: Known from Japan and the Russian Far East and introduced into the Nearctic (Grissell 2003).

Hosts.—*Osmia cornifrons*, *Osmia excavata*, and *Osmia taurus*, (Megachilidae) (Kamijo 1963, 1965).

Biology.—Iwata and Tachikawa (1966) reported a preponderance of females for rearings of this species from *Osmia taurus*. From 61 cocoons emerged 87 males and 726 females. The number of parasitoids per host (counted for 4 cocoons only) varied from 14 to 26.

Discussion.—Zerova and Romasenko (1986) key and figure this species in a paper on the parasitoids of megachilid bees in the former Soviet Union. Grissell (2003) illustrated the peculiar male head of this species based on specimens collected in Silver Spring, Montgomery County, Maryland, USA. *Monodontomerus japonicus* Ashmead was reported from *Osmia taurus*, but this record is undoubtedly a misidentification of *M. osmiae* (Grissell 1995). Males of this species are easily identified by the peculiar head (Figs 21, 22). Females have the discal area entirely setose.

Monodontomerus parkeri Grissell

Distribution.—NEARCTIC: Known from widespread localities in western North America stretching from Alberta, Canada to New Mexico, USA.

Host.—*Anthophora occidentalis* (Apidae).

Discussion.—*Monodontomerus parkeri* appears most similar to *M. tepedinoi* and their separation is discussed under the latter species. This species is also easily confused with *M. montivagus*. Males of the two species may be readily distinguished by comparing scapes: in *M. parkeri* the scape is laterally compressed and asymmetrically bent with the apex enlarged and a polished, depressed area on its outer side that continues onto the ventral surface (somewhat as in Fig. 57); in *M. montivagus* the scape is dorsoventrally compressed, symmetrically bent, and has the polished area completely ventral (Fig. 56). Additionally, in both sexes of *M. parkeri*, the apex of the costal cell dorsally has few setae (0 to 3 as in Fig. 43) whereas in *M. montivagus* there is a dorsal row of setae in the apical half to quarter (as in Fig. 31), and the transepim-

eral sulcus is complete (Fig. 54), whereas in *M. montivagus* it is not (Fig. 55). There are several less obvious and more relative characters that are difficult to use without comparative material. In *M. parkeri* the frenal area appears medially polished under reflected light even though it is sculptured, whereas in *M. montivagus* this area is generally entirely sculptured. In *M. parkeri* the admarginal wing area contains a few, widespaced setae (Fig. 44), and relatively few setae (3 to 5) are directly adjacent to the marginal vein (so that there is no setal row parallel to the vein), but in *M. montivagus* this area is evenly setose to the marginal vein (as in Fig. 43); there are enough setae to form a row parallel to the vein.

Monodontomerus rugulosus Thomson

Distribution.—PALEARCTIC: Widespread in western and central Europe (Zerova and Seryogina 2002).

Hosts.—This species has been reared from *Megachile rotundata* (Megachilidae) (Zerova and Romasenko 1986).

Biology.—This is a gregarious parasitoid in cocoons of its host.

Discussion.—*Monodontomerus rugulosus* appears quite similar to *M. argentinus*, but the two species occur in different, widely spaced zoogeographic regions. They may be separated by characters given in the key.

Monodontomerus tepedinoi Grissell

Distribution.—NEARCTIC: Known from Oregon and Utah, USA.

Hosts.—The species has been reared from *Osmia lignaria* (Megachilidae).

Discussion.—Females of *M. tepedinoi* are easily confused with *M. montivagus* and *M. parkeri*. From *M. montivagus* it is most readily separated by the upper anterior margin of the costal cell with only 1 to 3 setae at the apex (as in Fig. 43), whereas in *M. montivagus* the upper anterior margin has a setal row in its apical 1/4 to 1/3 (as in Fig. 31). From *M. parkeri* it is separated by the longer ovipositor (ca. 1.5 to almost 2× the metasomal length; 1 to 1.2× in *M. parkeri*) and by the scape, which has some metallic green color at least ventrally (all yellow to orange in *M. parkeri*). Males of *M. tepedinoi* are easier to distinguish than females based on the antenna as described in the key and compared in Figs 56, 57, 58). *Monodontomerus tepedinoi* is so far associated only with Megachilidae and *M. parkeri* with Apidae.

Monodontomerus thorpi Grissell

Distribution.—NEARCTIC: Known from isolated localities in southern California, Arizona, and western Texas, USA.

Hosts.—Reared from nests of *Anthidium maculatum* (Megachilidae).

Discussion.—This species has been reared from twig nests in the eastern and western extremes of its distribution. It is one of the easiest species of the genus to identify in both sexes as it is the only species to have the first two flagellar segments reduced (i.e., ring-like, Fig. 19), whereas all other species have only the first segment reduced (Fig. 20). Additionally, the hind femur is enlarged with only a ventral angle (Fig. 36) as opposed to other species that have a distinct tooth (Figs 37, 38).

Monodontomerus torchioi Grissell

Distribution.—NEARCTIC: The species is known only from Utah, USA.

Hosts.—Reared from nests of *Osmia lignaria* and *O. sanrafaelae* (Megachilidae).

Discussion.—*Monodontomerus torchioi* is easily confused with *M. montivagus*, *M. tepedioni*, and *M. parkeri* in females. The diagnostic characters used to separate these three taxa are given in key couplets 15 and 24–25 and under the discussion of the species mentioned.

Pseudotorymus Masi

Recognition.—Anterior margin of metapleuron straight (as in Fig. 2); occipital carina medially arched and midway be-

tween the hind ocelli and occipital foramen (as in Fig. 17); hind femur ventrally with a slight indication of a tooth; marginal vein long, 3 to 7× length of postmarginal vein and at least 6× length of stigmal vein.

Number of Species.—43.

Number Associated with Bees.—1 (questionably).

Distribution.—The genus is most abundant in the Palearctic Region (30 species) where its species are widespread and extend into northern Africa. It is also known from the Afrotropical Region (7 species) from Madagascar, Mali, Mozambique, Nigeria, Rwanda (Republic of the Congo), Senegal, South Africa, and Sudan. There are 4 species known from India in the Oriental Region and a single, widespread species is known from the Nearctic (southern Canada and northern USA).

Hosts.—Members have a broad host association including Curculionidae (Coleoptera) in leguminous seed pods; Bruchidae (Coleoptera) from galls on Asteraceae, Combretaceae, Fabaceae, Orchidaceae, and Rubiaceae; Cecidomyiidae (Diptera) associated with Apiaceae, Cruciferae, Fabaceae, Lamiaceae, Rosaceae, Salicaceae, and Scrophulariaceae; Eurytomidae (Hymenoptera) in grass stems (Poaceae); Cynipidae (Hymenoptera) in pods of Papaveraceae; Tenthredinidae (Hymenoptera); and Pyralidae (Lepidoptera).

Discussion.—The inclusion of this genus in relation to bee hosts is highly questionable and is based upon the single record for *P. indicus* as indicated below. Among the other 42 known species of *Pseudotorymus* the use of bees is unknown so this record is likely to be incorrect.

Pseudotorymus indicus (Mani)

Distribution.—This species is known only from southern India (Uttar Pradesh, Tamil Nadu) (Mani 1989).

Hosts.—The type series was reared from "flower bud galls" on *Dalbergia sissoo* (Fabaceae). Mani (1989) listed the host as a "leafcutting bee".

Discussion.—In light of the original rearing and the entire host range given above, I am inclined to dismiss this record until it can be reconfirmed.

Torymus Walker

Recognition.—This genus is easily recognized by the anterior edge of the metapleuron (usually its upper half) projecting forward as a lobe into the mesepimeron which is subdivided into upper and lower sections, the lower of which is delimited by an anterior groove (Fig. 1, compare with Fig. 2, arrows).

Number of Species.—Approximately 375.

Number Associated with Bees.—3.

Distribution.—All zoogeographic regions except Australia where it was apparently introduced (Grissell 1995).

Hosts of Genus.—Members of this genus are mostly parasitoids of larvae of gall-forming Diptera and Hymenoptera. A few have been reared from bees, and a few are phytophagous in seeds.

Discussion.—Until 1998 the species that parasitized bees were treated as the genus *Diomorus* Walker. Graham and Gijswijt (1998) synonymized *Diomorus* under *Torymus*, dividing its members into several species groups of the latter.

Torymus armatus (Boheman)

Distribution.—This species is widespread in the Palearctic, being reported from Europe (Graham and Gijswijt 1998) and Japan (Kamijo 1979). It was possibly introduced into Papua New Guinea (Bouček 1988).

Hosts.—Kamijo (1979) reported *T. armatus* from *Ceratina japonica* (Apidae) in *Rubus* twigs (Rosaceae) in Japan.

Discussion.—This species has reportedly been reared from several genera of Crabronidae, including *Rhopalum* (Box 1920) and *Crossocerus* (Gijswijt 1974), and seems to be associated with wasps and bees that

nest in the stems of *Rubus* (Graham and Gijswijt 1998). It is the most distinct of the three *Torymus* species known from bees, having the hind coxa dorsally bare and smooth, and the propodeum without carinae.

Toymus cupreus (Spinola)

Distribution.—The species is widespread in the Palearctic (Nikol'skaya and Zerova 1978), mostly in the "southern parts and middle of Europe" and reaching into the Netherlands (Graham and Gijswijt 1998). It is reported from Burma in the Oriental Region (Mani and Kaul 1972).

Host.—The original hosts given by Spinola included 7 species of cynipid galls, but these all probably housed aculeate bees or wasps. Mani and Kaul (1972) reported the species as "widely distributed as [a] parasitoid of *Osmia* sp. (Megachilidae) and Sphecidae."

Biology.—Enslin (1922) illustrated and discussed the larval and pupal stages of this species (as *Diomorus kollari*).

Discussion.—This Palearctic species and the following Nearctic species are geographically separated but show no morphological differences. In coloration, however, they are distinct as explained in key couplet 3.

Torymus zabriskii (Cresson)

Distribution.—The species is widespread in the United States.

Hosts.—The only reported bee host is *Ceratina dupla* (Apidae) (Zabriskei 1890).

Biology.—Krombein (1964) reported some short biological notes on this species (as *Diomorus*) as a parasitoid of *Ectemnius paucimaculatus* (Crabronidae). He suggested that *T. zabriskii* parasitized several cells in a succession of cells and that oviposition was probably through the wall of the plant stem (*Hibiscus*: Malvaceae) in which the wasp nested.

Discussion.—*Ceratina*, the only reported bee host (Zabriskei 1890), has been listed in the secondary literature several times but has never been reconfirmed. A number of other hosts in the family Crabronidae have been reported for this species including *Ectemnius*, *Crossocerus*, and *Rhopalum* (summarized by Grissell 1995).

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APPENDIX

Two lists are presented: bee host/chalcidoid and chalcidoid/bee host. The bee host list presents names as they currently are applied in the literature (i.e., valid names), not as they were originally published. The lists are derived from Bouček (1974), Noyes (2003), and Grissell (1995, 2000, 2005). Authors' names are given for bee host in the first list; chalcidoid authors are given in the subsequent list. The placement of bee genera in families is based on an electronic version (http://faculty.ucr.edu/~heraty/beepage.html) of Michener (2000).

Bee Host/Chalcidoid

Apidae

Allodape exoloma Strand: *Xylencyrtus tridens*

Allodape mucronata Smith: *Xylencyrtus tridens*

Allodape panurgoides Smith: *Xylencyrtus tridens*

Allodape rufogastra Lepeletier and Serville: *Xylencyrtus tridens*

Allodapula grandiceps (Friese): *Xylencyrtus tridens*

Allodapula melanopus (Cameron): *Xylencyrtus mumifex*

Ancyloscelis apiformis (F.): *Monodontomerus mexicanus*

Anthophora abrupta Say: *Melittobia acasta*, *Melittobia megachilis*, *Pediobius williamsoni*, *Monodontomerus mandibularis*, *Monodontomerus montivagus*

Anthophora bomboides bomboides Kirby: *Leucospis gigas*, *Monodontomerus mandibularis*, *Monodontomerus montivagus*

Anthophora bomboides neomexicana Cockerell: *Monodontomerus montivagus*

Anthophora linsleyi Timberlake: *Monodontomerus montivagus*

Anthophora marginata Smith: *Monodontomerus mexicanus*

Anthophora occidentalis Cresson: *Monodontomerus montivagus*, *Monodontomerus parkeri*

Anthophora plumipes (Pallas): *Monodontomerus obscurus*

Anthophora retusa (L.): *Melittobia acasta, Melittobia pelopoei, Monodontomerus aeneus*
?*Anthophora vallorum* (Cockerell): *Monodontomerus montivagus*
Apis cerana (F.): *Antrocephalus* sp.
Apis mellifera L.: *Dibrachys boarmiae, Melittobia acasta, Monodontomerus laticornis, Nasonia vitripennis, Pteromalus apum, Tetrastichus howardi*
Bombus agrorum F.: *Pteromalus conopidarum*
Bombus americanorum F.: *Pediobius williamsoni*
Bombus atratus Franklin: *Pediobius williamsoni*
Bombus fervidus F.: *Melittobia chalybii*
Bombus hortorum (L.): *Melittobia acasta*
Bombus lapidarius (L.): *Pteromalus conopidarum*
Bombus morrisoni Cresson: *Monodontomerus montivagus*
Bombus ruderatus (F.): *Melittobia acasta*
Bombus sp.: *Dibrachys cavus, Melittobia hawaiiensis, Pachycrepoideus vindemmiae*
Bombus terrestris (L.): *Melittobia acasta*
Braunsapis leptozonia (Vachal): *Xylencyrtus tridens*
Braunsapis rolini (Vachal): *Echthrodape africana*
Braunsapis rufipes (Friese): *Echthrodape africana*
Braunsapis simplicipes Michener: *Echthrodape africana*
Braunsapis unicolor Smith: *Echthrodape papuana*
Centris analis F.: *Leucospis cayennensis*
Centris bicornuta Mocsary: *Leucospis cayennensis*
Centris nitida Smith: *Leucospis cayennensis*
Centris tarsata (Smith): *Leucospis cayennensis*
Centris vittata Lepeletier: *Leucospis cayennensis*
Ceratina calcarata Robertson: *Axima zabriskiei*
Ceratina callosa (F.): *Eurytoma nodularis, Monodontomerus aeneus*
Ceratina dallatorreana Friese: *Eurytoma apiculae*
Ceratina dupla Say: *Axima zabriskiei, Baryscapus americanus, Habritys latrus, Torymus zabriskii*
Ceratina flavipes Smith: *Neochalcis breviceps*
Ceratina ignara Cresson: *Baryscapus americanus*
Ceratina japonica Cockerell: *Cleonymus ceratinae, Torymus armatus*
Ceratina nanula Cockerell: *Baryscapus americanus, Eurytoma apiculae*
Ceratina punctigena Cockerell: *Eurytoma apiculae*
Ceratina sequoiae Michener: *Baryscapus americanus*
Ceratina sp.: *Cheiloneurus leptulus, Epistenia coeruleata, Melittobia megachilis, Micrapion dalyi, Micrapion nasutum, Micrapion richardsi*
Ceratina truncata Friese: *Micrapion steffani*
?*Ctenoplectra chalybea* Smith: *Leucospis histrio*
Diadasina distincta (Holmberg): *Leucospis genalis*
Eufriesea nigrescens (Friese): *Monodontomerus argentinus*
Euglossa annectans Dressler: *Melittobia* sp.
Euglossa ignita Smith: *Polistomorpha fasciata*
Euglossa sp.: *Polistomorpha conura, Polistomorpha fasciata*
Eulaema meriana (Oliver): *Leucospis pinna*
?*Melissodes* sp.: *Monodontomerus montivagus*
Melitoma taurea (Say): *Monodontomerus mandibularis*
Trigona sp.: *Brachymeria discreta*
Xylocopa brasilianorum (L.): *Leucospis klugii*
Xylocopa caerulea (F.): *Coelopencyrtus pallidiceps*
Xylocopa caffra (L.): *Coelopencyrtus callainus, Coelopencyrtus taylori*
Xylocopa divisa Klug: *Coelopencyrtus callainus, Coelopencyrtus taylori*
Xylocopa fenestrata (F.): *Monodontomerus obscurus*
Xylocopa flavicollis (De Geer): *Coelopencyrtus callainus*
Xylocopa flavorufa (De Geer): *Coelopencyrtus callainus, Coelopencyrtus taylori, Coelopencyrtus watmoughi*
Xylocopa frontalis (Oliver): *Coelopencyrtus gargaris*
Xylocopa inconstans Smith: *Coelopencyrtus callainus*
Xylocopa nogueirai Hurd and Moure: *Leucospis xylocopae*
Xylocopa pubescens Spinola: *Coelopencyrtus* sp.
Xylocopa scioensis Gribodo: *Coelopencyrtus cyprius*
Xylocopa sp.: *Leucospis reversa*
Xylocopa submordax Cockerell: *Leucospis anthidioides*
Xylocopa sulcatipes Maa: *Coelopencyrtus* sp.
Xylocopa tabaniformis orpifex Smith: *Monodontomerus montivagus*
Xylocopa tenuiscapa Westwood: *Coelopencyrtus krishnamurtii*
Xylocopa tranquebarorum (Swederus): *Melittobia sosui*
Xylocopa turanica Morawitz: *Melittobia acasta*
Xylocopa watmoughi Eardly: *Coelopencyrtus* sp.

Colletidae

Hylaeus communis Nylander: *Coelopencyrtus arenarius, Coelopencyrtus callidii*
Hylaeus cressoni Cockerell: *Coelopencyrtus hylaei*
Hylaeus ellipticus (Kirby): *Coelopencyrtus hylaeoleter*
Hylaeus fuscipennis (Smith): *Coelopencyrtus kaalae*

Hylaeus heraldicus (Smith): *Coelopencyrtus nothylaei*
Hylaeus koae (Perkins): *Coelopencyrtus kaalae*
Hylaeus nigritus (F.): *Coelopencyrtus arenarius*
Hylaeus polifolii Cockerell: *Eurytoma stigmi*
Hylaeus pubescens (Perkins): *Coelopencyrtus kaalae, Coelopencyrtus sexramosus*
Hylaeus sp.: *Eurytoma nodularis, Melittobia acasta, Melittobia hawaiiensis*
Hylaeus varifrons Cresson: *Pteromalus analis*

Halictidae

Halictus africanus Friese: *Aperilampus varians*
?*Lasioglossum pruinosum* (Robertson): *Eupelmus ashmeadi, Eupelmus rhizophelus*
Nomia melanderi Cockerell: *Mesopolobus bruchophagi*

Megachilidae

Anthidiellum perplexum Smith: *Leucospis affinis*
Anthidiellum sp.: *Leucospis slossonae*
Anthidiellum strigatum (Panzer): *Leucospis bifasciata, Leucospis dorsigera*
Anthidium collectum Huard: *Monodontomerus montivagus*
Anthidium diadema Latreille: *Leucospis dorsigera*
Anthidium emarginatum (Say): *Leucospis affinis, Leucospis dorsigera, Monodontomerus montivagus*
Anthidium florentinum (F.): *Melittobia acasta, Monodontomerus aeneus, Monodontomerus laticornis*
Anthidium maculatum Smith: *Monodontomerus thorpi*
Anthidium maculosum Cresson: *Leucospis affinis*
Anthidium ?*mormonum* Cresson: *Monodontomerus montivagus*
Anthidium septemspinosum Lepeletier: *Monodontomerus laticornis*
Ashmeadiella aridula astragali Michener: *Leucospis affinis*
Ashmeadiella bigeloviae (Cockerell): *Microdontomerus parkeri*
Ashmeadiella californica (Ashmead): *Monodontomerus montivagus*
Ashmeadiella cubiceps (Cresson): *Microdontomerus parkeri*
Ashmeadiella gillettei Titus: *Microdontomerus parkeri*
Ashmeadiella meliloti Cockerell: *Leucospis affinis*
Ashmeadiella rufipes Titus: *Microdontomerus parkeri*
Coelioxys octodentata Say: *Aprostocetus* sp., *Merisus* sp., *Tetrastichus coelioxydis*
?*Coelioxys quadridentatus* (L.): *Leucospis gigas*
Dianthidium curvatum sayi Cockerell: *Monodontomerus montivagus*
Dianthidium heterulkei Schwarz: *Monodontomerus clementi*
Dianthidium pudicum pudicum (Cresson): *Leucospis affinis, Monodontomerus montivagus*
Dianthidium pudicum consimile (Ashmead): *Microdontomerus anthidii, Monodontomerus montivagus*
Dianthidium sp.: *Monodontomerus dianthidii*
Heriades crenulatus Nylander: *Eurytoma heriadi, Melittobia acasta*
?*Heriades* sp.: *Leucospis dorsigera*
Heriades truncorum (L.): *Melittobia acasta*
Hoplitis acuticornis (Dufour and Perris): *Leucospis biguetina*
Hoplitis adunca (Panzer): *Eurytoma nodularis, Leucospis dorsigera, Melittobia acasta, Monodontomerus aeneus, Monodontomerus obscurus*
Hoplitis anthocopoides (Schenck) (nest): *Monodontomerus montivagus*
Hoplitis bullifacies Michener: *Microdontomerus enigma, Microdontomerus parkeri*
Hoplitis palmarum (Cockerell): *Microdontomerus parkeri*
Hoplitis producta (Cresson): *Cleonymus amabilis, Eurytoma amplicoxa, Eurytoma stigmi, Leucospis affinis*
Hoplitis tridentata (Dufour and Perris): *Leucospis biguetina, Neochalcis osmicida*
Hoplosmia ligurica (Morawitz): *Leucospis dorsigera*
Lithurgus capensis Friese: *Leucospis ornata, Leucospis varicollis*
Megachile aetheria Mitchell: *Melittobia hawaiiensis*
Megachile albitarsis Cresson: *Ablaxia cupraeus*
Megachile apicalis Spinola: *Monodontomerus aeneus*
Megachile argentata (F.): *Dibrachys cavus, Melittobia acasta, Monodontomerus obscurus*
Megachile bombycina Radoszkowski: *Melittobia acasta*
Megachile brevis Say: *Aprostocetus* sp., *Cricellius megachilis, Leucospis affinis, Melittobia chalybii, Merisus* sp., *Microdontomerus parkeri, Tetrastichus coelioxydis*
Megachile centuncularis (L.): *Ablaxia cupraeus, Anagrus putnamii, Aprostocetus pygmaeus, Baryscapus megachilidis, Dibrachys* sp., *Melittobia acasta, Melittobia chalybii, Melittobia megachilis,*

Monodontomerus aeneus, Monodontomerus laticornis, Monodontomerus montivagus, Monodontomerus obscurus, Pteromalus apum, Pteromalus macronychivorus

Megachile cephalotes Smith: *Monodontomerus obscurus*

Megachile concinna Smith: *Baryscapus megachilidis, Melittobia australica, Monodontomerus aeneus*

Megachile disjunctiformis Cockerell: *Leucospis japonica*

Megachile ericetorum Lepeletier: *Leucospis dorsigera*

Megachile flavipes Spinola: *Monodontomerus obscurus*

Megachile gentilis Cresson: *Baryscapus megachilidis, Leucospis affinis*

Megachile gomphrenae Holmberg: *Melittobia hawaiiensis*

Megachile gratiosa Cameron: *Melittobia* sp.

Megachile hungarica Gerstaecker: *Leucospis gigas*

Megachile inermis Provancher: *Leucospis affinis, Melittobia chalybii*

Megachile lanata (F.): *Melittobia australica, Monodontomerus obscurus*

Megachile mendica Cresson: *Leucospis affinis*

Megachile montivaga Cresson: *Leucospis affinis, Microdontomerus apianus*

Megachile nipponica Cockerell: *Leucospis japonica*

Megachile pallefacta Vachal: *Melittobia hawaiiensis*

Megachile palmarum Perkins: *Melittobia hawaiiensis*

Megachile parietina (Geoffrey): *Leucospis gigas, Melittobia acasta, Monodontomerus aeneus, Monodontomerus obscurus*

Megachile peruviana Smith: *Monodontomerus mexicanus*

Megachile poeyi Guérin-Méneville: *Leucospis poeyi*

Megachile pugnata Say: *Dibrachys* sp., *Leucospis affinis, Melittobia* sp., *Monodontomerus bakeri*

Megachile pyrenaica Lepeletier: *Leucospis gigas, Pteromalus apum*

Megachile rancaguensis Friese: *Leucospis hopei*

Megachile rangii Cheesman: *Leucospis aruina*

Megachile relativa Cresson: *Dibrachys relativus, Leucospis affinis, Melittobia acasta, Melittobia chalybii, Monodontomerus bakeri, Monodontomerus montivagus, Pteromalus apum*

Megachile rotundata (F.): *Baryscapus daira, Baryscapus megachilidis, Dibrachys confusus, Dibrachys maculipennis, Melittobia acasta, Melittobia australica, Melittobia chalybii, Melittobia hawaiiensis, Monodontomerus aeneus, Monodontomerus bakeri, Monodontomerus clementi* (in lab), *Monodontomerus laticornis, Monodontomerus montivagus, Monodontomerus obscurus, Monodontomerus rugulosus, Pteromalus apum, Pteromalus conopidarum, Pteromalus veneris, Tetrastichus* sp.

Megachile sculpturalis Smith: *Leucospis japonica*

Megachile sicula Rossi: *Leucospis gigas, Monodontomerus aeneus*

Megachile sp.: *Brachymeria paraguayensis, Calosota fumipennis, Horismenus albipes, Kocourekia clavigera, Leucospis histrio, Leucospis intermedia, Melittobia pelopoei, Monodontomerus acrostigmus, Monodontomerus argentinus*

Megachile spissula (Cockerell): *Lariophagus obtusus, Melittobia acasta*

Megachile ustulatum (Smith): *Leucospis histrio*

Megachile willowmorensis Brauns: *Leucospis ornata*

Megachile willughbiella (Kirby): *Melittobia acasta, Monodontomerus obscurus, Pteromalus apum*

Megachile xylocopoides Smith: *Baryscapus megachilidis*

Megachile zaptlana Cresson: *Melittobia australica*

Microthurge corumbae (Cockerell): *Leucospis* sp.

Osmia atriventris Cresson: *Leucospis affinis*

Osmia bicolor (Schrank): *Eulophus osmiarum*

Osmia bicornis (Schrank): *Leucospis dorsigera, Leucospis gigas*

Osmia brevicornis (F.): *Monodontomerus aeneus*

Osmia californica Cresson: *Leucospis affinis*

Osmia "coerulea" [?*lapsus* for *O. coerulescens*, Baur and Amiet 2000]: *Leucospis gigas*

Osmia coerulescens (L.): *Aprostocetus pygmaeus, Eurytoma nodularis, Leucospis gigas, Monodontomerus aeneus*

Osmia coloradensis Cresson: *Monodontomerus bakeri*

Osmia cordata Robertson: *Monodontomerus mandibularis, Monodontomerus montivagus, Monodontomerus obscurus*

Osmia cornifrons Radoszkowski: *Monodontomerus obscurus, Monodontomerus osmiae*

Osmia cornuta (Latreille): *Leucospis dorsigera, Monodontomerus aeneus*

Osmia emarginata Lepeletier: *Leucospis intermedia, Monodontomerus aeneus*

Osmia excavata Alfken: *Leucospis japonica, Monodontomerus osmiae*

Osmia fedtschenkoi (Morawitz): *Leucospis dorsigera*

Osmia fulviventris (Panzer): *Leucospis dorsigera, Monodontomerus aeneus*

Osmia globicola (Stadelmann): *Leucospis osmiae*

Osmia kincaidii Cockerell: *Leucospis affinis*, *Monodontomerus montivagus*
Osmia latisulcata Michener: *Monodontomerus montivagus*
Osmia latreillei (Spinola): *Calosota vernalis*, *Monodontomerus aeneus*, *Monodontomerus obscurus*
Osmia leucomelana (Kirby): Eurytoma sp., Melittobia acasta
Osmia lignaria Say: *Monodontomerus montivagus*, *Monodontomerus obscurus*, *Monodontomerus tepedinoi*, *Monodontomerus torchioi*
Osmia marginata Michener: *Microdontomerus parkeri*
Osmia nigrifrons Cresson: *Dibrachys pelos*, *Monodontomerus aeneus*
Osmia niveata (F.): *Leucospis dorsigera*
Osmia parietina Curtis: *Leucospis dorsigera*
Osmia parvula Dufour and Perris: *Eurytoma nodularis*
Osmia pumila Cresson: *Leucospis affinis*
Osmia ribifloris Cockerell: *Monodontomerus brevicrus*, *Monodontomerus montivagus*, *Monodontomerus obscurus*
Osmia rostrata Sandhouse: *Leucospis affinis*
Osmia rufa cornigera (Rossi): *Monodontomerus aeneus*, *Monodontomerus obscurus*
Osmia rufa rufa (L): *Leucospis dorsigera*, *Leucospis gigas*, *Melittobia acasta*, *Monodontomerus aeneus*, *Monodontomerus obscurus*
Osmia sanrafaelae Parker: *Monodontomerus montivagus*, *Monodontomerus obscurus*, *Monodontomerus torchioi*
Osmia simillima Smith: *Leucospis affinis*
Osmia sp.: *Epistenia coeruleata*, *Monodontomerus montivagus* (cocoon in *Trypargilum politum* nest), *Torymus cupreus*
Osmia submicans Morawitz: *Monodontomerus aeneus*
Osmia taurus Smith: *Leucospis japonica*, *Monodontomerus osmiae*
Osmia texana Cresson: *Monodontomerus bakeri*, *Monodontomerus montivagus*
Osmia tricornis Latreille: *Leucospis dorsigera*, *Monodontomerus aeneus*
Pachyanthidium cordatum (Smith): *Leucospis tricolor*
Pachyanthidium truncataum (Smith): *Leucospis tricolor*
Pseudoanthidium lituratum (Panzer): *Adontomerus gregalis*, *Adontomerus nesterovi*, *Neochalcis fertoni*
Rhodanthidium sticticum (F.): *Monodontomerus anthidiorum*
Serapista denticulata (Smith): *Leucospis africana*, *Leucospis tricolor*
Stelis depressa Timberlake: *Monodontomerus montivagus*
Stelis nasuta Latreille: *Melittobia acasta*, *Monodontomerus aeneus*
Stelis sexmaculata Ashmead: *Cleonymus amabilis*, *Leucospis affinis*

Chalcidoid/Bee Host

Chalcididae

Antrocephalus sp.: *Apis cerana*
Brachymeria discreta Gahan: *Trigona* sp.
Brachymeria paraguayensis Girault: *Megachile* sp.
Neochalcis breviceps (Masi): *Ceratina flavipes*
Neochalcis fertoni (Kieffer): *Pseudoanthidium lituratum*
Neochalcis osmicida (Saunders): *Hoplitis tridentata*

Encyrtidae

Cheiloneurus leptulus Annecke and Prinsloo: *Ceratina* sp.
Coelopencyrtus arenarius (Erdös): *Hylaeus communis*, *Hylaeus nigritus*
Coelopencyrtus callainus Annecke: *Xylocopa caffra*, *Xylocopa divisa*, *Xylocopa flavicollis*, *Xylocopa flavorufa*, *Xylocopa inconstans*
Coelopencyrtus callidii (Jansson): *Hylaeus communis*
Coelopencyrtus cyprius Annecke: *Xylocopa scioensis*
Coelopencyrtus gargaris (Walker): *Xylocopa frontalis*
Coelopencyrtus hylaei Burks: *Hylaeus cressoni*
Coelopencyrtus hylaeoleter Burks: *Hylaeus ellipticus*
Coelopencyrtus kaalae (Ashmead): *Hylaeus fusci-pennis*, *Hylaeus koae*, *Hylaeus pubescens*
Coelopencyrtus krishnamurtii (Mahdihassan): *Xylocopa tenuiscapa*
Coelopencyrtus nothylaei Annecke: *Hylaeus heraldicus*
Coelopencyrtus pallidiceps (Girault): *Xylocopa caerulea*
Coelopencyrtus sexramosus Timberlake: *Hylaeus pubescens*
Coelopencyrtus sp.: *Xylocopa pubescens*, *Xylocopa sulcatipes*, *Xylocopa watmoughi*
Coelopencyrtus taylori Annecke and Doutt: *Xylocopa caffra*, *Xylocopa divisa*, *Xylocopa flavorufa*

Coelopencyrtus watmoughi Annecke: *Xylocopa flavorufa*

Eulophidae

Aprostocetus pygmaeus Zetterstedt: *Megachile centuncularis, Osmia coerulescens*
Aprostocetus sp.: *Coelioxys octodentata, Megachile brevis*
Baryscapus americanus (Ashmead): *Ceratina dupla, Ceratina iguana, Ceratina nanula, Ceratina sequoiae*
Baryscapus daira (Walker): *Megachile rotundata*
Baryscapus megachilidis (Burks): *Megachile centuncularis, Megachile concinna, Megachile gentilis, Megachile rotundata, Megachile xylocopoides*
Eulophus osmiarum Robineau-Desvoidy: *Osmia bicolor*
Horismenus albipes (Schrottky): *Megachile* sp.
Kocourekia clavigera Bouček: *Megachile* sp.
Melittobia acasta (Walker): *Anthidium florentinum, Anthophora abrupta, Anthophora retusa, Apis mellifera, Bombus hortorum, Bombus ruderatus, Bombus terrestris, Heriades crenulatus, Heriades truncorum, Hoplitis adunca, Hylaeus* sp., *Megachile argentata, Megachile bombycina, Megachile centuncularis, Megachile parietina, Megachile relativa, Megachile rotundata, Megachile spissula, Megachile willughbiella, Osmia leucomelana, Osmia rufa, Stelis nasuta, Xylocopa turanica*
Melittobia australica Girault: *Megachile concinna, Megachile lanata, Megachile rotundata, Megachile zaptlana*
Melittobia chalybii Ashmead: *Bombus fervidus, Megachile brevis, Megachile centuncularis, Megachile inermis, Megachile relativa, Megachile rotundata*
Melittobia hawaiiensis Perkins: *Bombus* sp., *Hylaeus* sp., *Megachile aetheria, Megachile gomphrenae, Megachile pallefacta, Megachile palmarum, Megachile rotundata*
Melittobia megachilis (Packard): *Anthophora abrupta, Ceratina* sp., *Megachile centuncularis*
Melittobia pelopoei [unavailable name]: *Anthophora retusa, Megachile* sp.
Melittobia sosui Dahms: *Xylocopa tranquebarorum*
Melittobia sp.: *Euglossa annectans, Megachile gratiosa, Megachile puguata*
Pediobius williamsoni Girault: *Anthophora abrupta, Bombus americanorum, Bombus atratus*
Tetrastichus coelioxydis (Burks): *Coelioxys octodentata, Megachile brevis*
Tetrastichus howardi (Olliff): *Apis mellifera*
Tetrastichus sp.: *Megachile rotundata*
Torymus armatus (Boheman): *Ceratina japonica*
Torymus cupreus (Spinola): *Osmia* sp.
Torymus zabriskii (Cresson): *Ceratina dupla*
Xylencyrtus mumifex Annecke: *Allodapula melanopus*
Xylencyrtus tridens Annecke: *Allodape exoloma, Allodape mucronata, Allodape panurgoides, Allodape rufogastra, Allodapula grandiceps, Braunsapis leptozonia*

Eupelmidae

Calosota fumipennis Curtis: *Megachile* sp.
Calosota vernalis Curtis: *Osmia latreillei*
Eupelmus ashmeadi Melander and Brues: ?*Lasioglossum pruinosum*
Eupelmus rhizophelus Brues: ?*Lasioglossum pruinosum*

Eurytomidae

Axima zabriskiei Howard: *Ceratina calcarata, Ceratina dupla*
Eurytoma amplicoxa Bugbee: *Hoplitis producta*
Eurytoma apiculae Bugbee: *Ceratina dallatorreana, Ceratina nanula, Ceratina punctigena*
Eurytoma heriadi Zerova: *Heriades crenulatus*
Eurytoma nodularis Boheman: *Ceratina callosa, Hylaeus* sp., *Osmia adunca, Osmia coerulescens, Osmia parvula,*
Eurytoma sp.: *Osmia leucomelana*
Eurytoma stigmi Ashmead: *Hoplitis producta, Hylaeus polifolii*

Leucospidae

Leucospis affinis Say: *Anthidiellum perplexum, Anthidium emarginatum, Anthidium maculosum, Ashmeadiella aridula astragli, Ashmeadiella meliloti, Dianthidium pudicum, Hoplitis producta, Megachile brevis, Megachile gentilis, Megachile inermis, Megachile mendica, Megachile montivaga, Megachile pugnata, Megachile relativa, Osmia atriventris, Osmia californica, Osmia kincaidii, Osmia pumila, Osmia rostrata, Osmia simillima, Stelis sexmaculata.*
Leucospis africana Cameron: *Serapista denticulata*
Leucospis anthidioides Westwood: *Xylocopa submordax*
Leucospis aruina Walker: *Megachile rangii*
Leucospis bifasciata Klug: *Anthidiellum strigatum*
Leucospis biguetina Jurine: *Hoplitis acuticornis, Hoplitis tridentata*

Leucospis cayennensis Westwood: *Centris analis, Centris bicornuta, Centris nitida, Centris tarsata, Centris vittata*
Leucospis dorsigera F.: *Anthidiellum strigatum, Anthidium diadema, Anthidium emarginatum, ?Heriades* sp., *Hoplitis adunca, Hoplosmia ligurica, Megachile ericetorum, Osmia bicornis, Osmia cornuta, Osmia fedtschenkoi, Osmia fulviventris, Osmia niveata, Osmia parietina, Osmia rufa rufa, Osmia tricornis*
Leucospis genalis Bouček: *Diadasina distincta*
Leucospis gigas F.: *Anthophora bomboides bomboides, ?Coelioxys quadridentatus, Megachile hungarica, Megachile parietina, Megachile pyrenaica, Megachile sicula, Osmia bicornis, Osmia ?coerulescens, Osmia rufa rufa*
Leucospis histrio Maindron: *?Ctenoplectra chalybea, Megachile ustulatum*
Leucospis hopei Westwood: *Megachile rancaguensis*
Leucospis intermedia Illiger: *Megachile* sp., *Osmia emarginata*
Leucospis japonica Walker: *Megachile disjunctiformis, Megachile nipponica, Megachile sculpturalis, Osmia excavata, Osmia taurus*
Leucospis klugii Westwood: *Xylocopa brasilianorum*
Leucospis ornata Westwood: *Lithurgus capensis, Megachile willowmorensis*
Leucospis osmaie Bouček: *Osmia globicola*
Leucospis pinna Grissell and Cameron: *Eulaema meriana*
Leucospis poeyi Guérin-Méneville: *Megachile poeyi*
Leucospis reversa Bouček: *Xylocopa* sp.
Leucospis slossonae Weld: *Anthidiellum* sp.
Leucospis sp.: *Microthurge corumbae*
Leucospis tricolor Kirby: *Pachyanthidium cordatum, Pachyanthidium truncatum, Serapista denticulata*
Leucospis varicollis Cameron: *Lithurgus capensis*
Leucospis xylocopae Burks: *Xylocopa nogueirai*
Micrapion dalyi Bouček: *Ceratina* sp.
Micrapion nasutum Bouček: *Ceratina* sp.
Micrapion richardsi Bouček: *Ceratina* sp.
Micrapion steffani Bouček: *Ceratina truncata*
Polistomorpha conura Bouček: *Euglossa* sp.
Polistomorpha fasciata Westwood: *Euglossa ignita, Euglossa* sp.

Mymaridae

Anagrus putnamii Packard: *Megachile centuncularis*

Perilampidae

Aperilampus varians Strand: *Halictus africanus*

Pteromalidae

Ablaxia cupraeus (Provancher): *Megachile albitarsis, Megachile centuncularis*
Cleonymus amabilis Cockerell: *Hoplitis producta, Stelis sexmaculata*
Cleonymus ceratinae Kamijo: *Ceratina japonica*
Cricellius megachilis Ashmead: *Megachile brevis*
Dibrachys boarmiae (Walker): *Apis mellifera*
Dibrachys cavus (Walker): *Bombus* sp., *Megachile argentata*
Dibrachys confusus (Girault): *Megachile rotundata*
Dibrachys maculipennis Szelenyi: *Megachile rotundata*
Dibrachys pelos Grissell: *Osmia nigrifrons*
Dibrachys relativus Doganlar: *Megachile relativus*
Dibrachys sp.: *Megachile centuncularis, Megachile pugnata*
Epistenia coeruleata Westwood: *Ceratina* sp., *Osmia* sp.
Habritys latrus Wallace: *Ceratina dupla*
Lariophagus obtusus Kamijo: *Megachile spissula*
Merisus sp.: *Coelioxys octodentata, Megachile brevis*
Mesopolobus bruchophagi (Gahan): *Nomia melanderi*
Nasonia vitripennis (Walker): *Apis mellifera*
Pachycrepoideus vindemmiae Rondani: *Bombus* sp.
Pteromalus analis Ashmead: *Hylaeus varifrons*
Pteromalus apum (Retzius): *Apis mellifera, Megachile centuncularis, Megachile pyrenaica, Megachile relativa, Megachile rotundata, Megachile willughbiella*
Pteromalus conopidarum (Bouček): *Bombus agrorum, Bombus lapidarius, Megachile rotundata*
Pteromalus macronychivorus Perez: *Megachile centuncularis*
Pteromalus veneris Dalla Torre: *Megachile rotundata*

Torymidae

Adontomerus gregalis (Steffan): *Pseudoanthidium lituratum*
Adontomerus nesterovi Zerova: *Pseudoanthidium lituratum*
Echthrodape africana Burks: *Braunsapis rolini, Braunsapis rufipes, Braunsapis simplicipes*
Echthrodape papuana Bouček: *Braunsapis unicolor*

Microdontomerus anthidii (Ashmead): *Dianthidium pudicum consimile*

Microdontomerus apianus Grissell: *Megachile montivaga*

Microdontomerus enigma Grissell: *Hoplitis bullifacies*

Microdontomerus parkeri Grissell: *Ashmeadiella bigeloviae, Ashmeadiella cubiceps, Ashmeadiella gillettei, Ashmeadiella rufipes, Hoplitis bullifacies, Hoplitis palmarum, Megachile brevis, Osmia marginata*

Monodontomerus acrostigmus Grissell: *Megachile* sp.

Monodontomerus aeneus (F.): *Anthidium florentinum, Anthophora retusa, Ceratina callosa, Hoplitis adunca, Megachile apicalis, Megachile centuncularis, Megachile concinna, Megachile parietina, Megachile rotundata, Megachile sicula, Osmia brevicornis, Osmia coerulescens, Osmia cornigera, Osmia cornuta, Osmia emarginata, Osmia fulviventris, Osmia latreillei, Osmia rufa, Osmia nigrifrons, Osmia submicans, Osmia tricornis, Stelis nasuta*

Monodontomerus anthidiorum (Lucas): *Rhodanthidium sticticum*

Monodontomerus argentinus Brèthes: *Eufriesea nigrescens, Megachile* sp.

Monodontomerus bakeri Gahan: *Megachile pugnata, Megachile relativa, Megachile rotundata, Osmia coloradensis, Osmia texana*

Monodontomerus brevicrus Grissell: *Osmia ribifloris*

Monodontomerus clementi Grissell: *Dianthidium heterulkei, Megachile rotundata*

Monodontomerus dianthidii Gahan: *Dianthidium* sp.

Monodontomerus laticornis Grissell and Zerova: *Anthidium florentinum, Anthidium septemspinosum, Apis mellifera, Megachile centuncularis, Megachile rotundata*

Monodontomerus mandibularis Gahan: *Anthophora abrupta, Anthophora bomboides bomboides, Melitoma taurea, Osmia cordata*

Monodontomerus mexicanus Gahan: *Ancyloscelis apiformis, Anthophora marginata, Megachile peruviana*

Monodontomerus montivagus Ashmead: *Anthidium collectum, Anthidium emarginatum, Anthidium ?mormonum, Anthophora abrupta, Anthophora bomboides bomboides, Anthophora bomboides neomexicana, Anthophora linsleyi, ?Anthophora occidentalis, ?Anthophora vallorum, Ashmeadiella californica, Bombus morrisoni, Dianthidium curvatum sayi, Dianthidium pudicum consimile, Dianthidium pudicum, Hoplitis anthocopoides* (nest), *Megachile centuncularis, Megachile relativa, Megachile rotundata, ?Melissodes* sp., *Osmia cordata, Osmia kincaidii, Osmia latisulcata, Osmia lignaria, Osmia ribifloris, Osmia sanrafaelae, Osmia texana, Stelis depressa, Xylocopa tabaniformis orpifex*

Monodontomerus obscurus Westwood: *Anthophora plumipes, Hoplitis adunca, Megachile argentata, Megachile centuncularis, Megachile cephalotes, Megachile flavipes, Megachile lanata, Megachile parietina, Megachile rotundata, Megachile willughbiella, Osmia cordata, Osmia cornifrons, Osmia latreillei, Osmia lignaria, Osmia ribfloris, Osmia rufa rufa, Osmia rufa cornigera, Osmia sanrafaelae, Xylocopa fenestrata*

Monodontomerus osmiae Kamijo: *Osmia cornifrons, Osmia excavata, Osmia taurus*

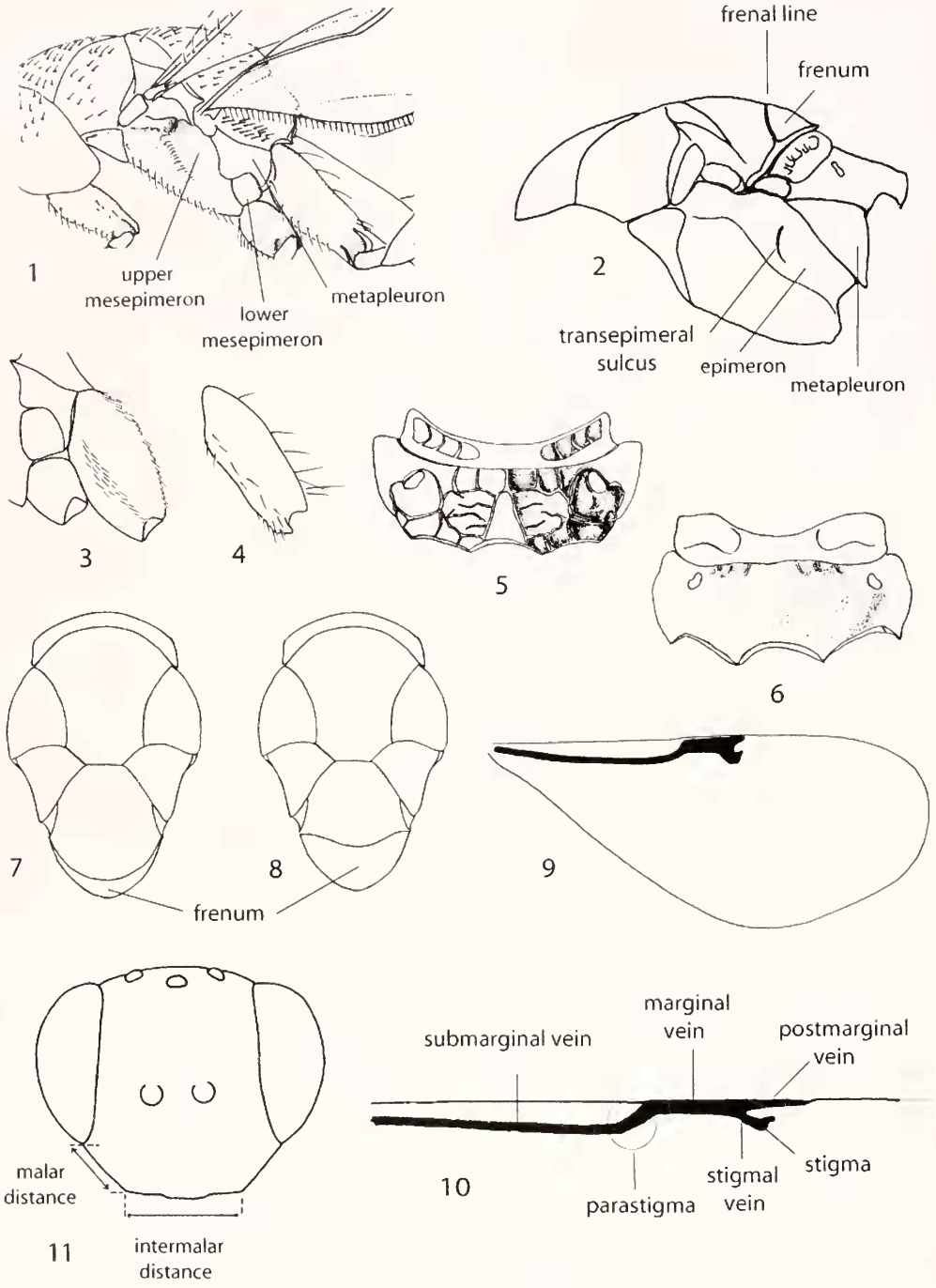
Monodontomerus parkeri Grissell: *Anthophora occidentalis*

Monodontomerus rugulosus Thomson: *Megachile rotundata*

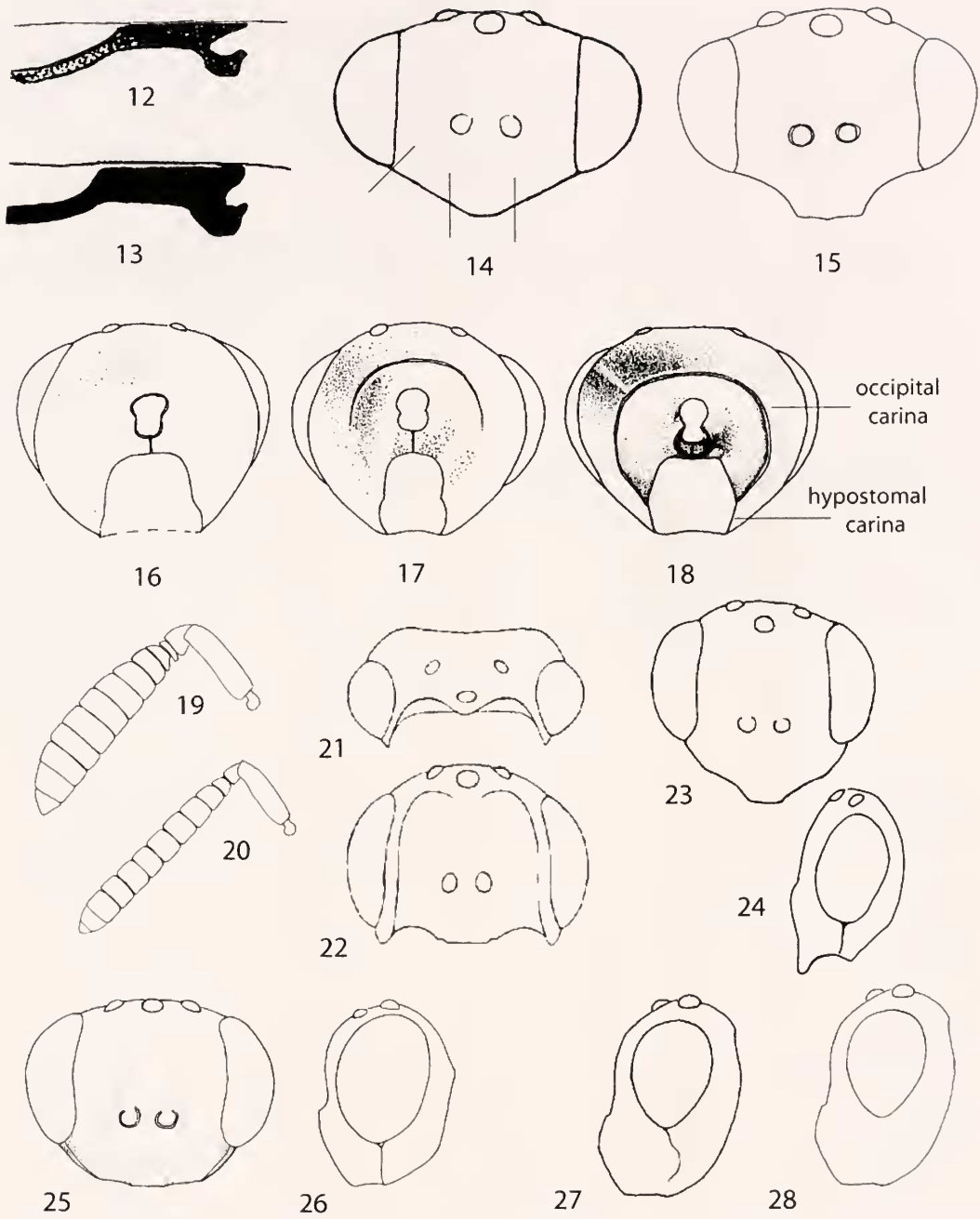
Monodontomerus tepedinoi Grissell: *Osmia lignaria*

Monodontomerus thorpi Grissell: *Anthidium maculatum*

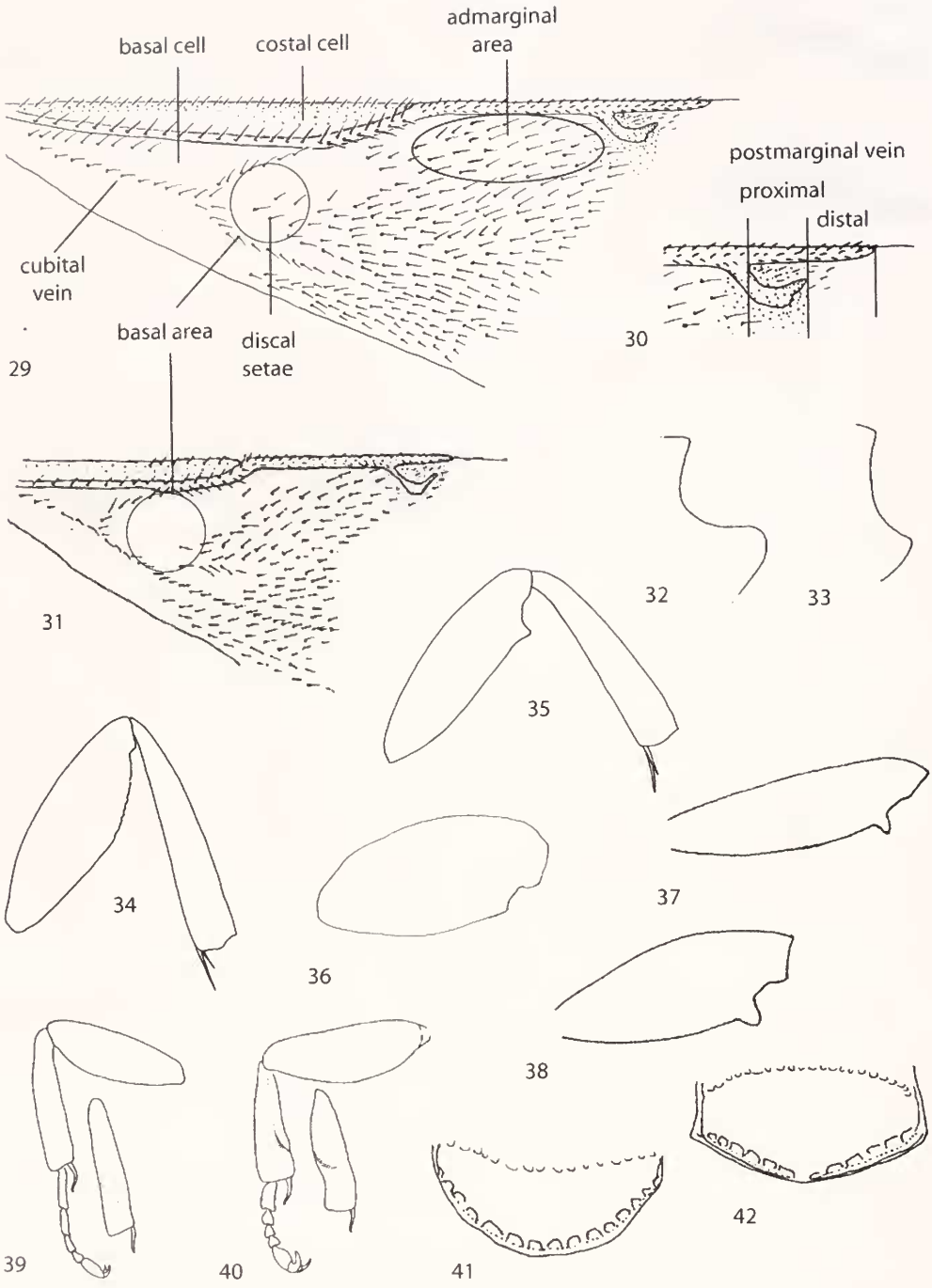
Monodontomerus torchioi Grissell: *Osmia lignaria, Osmia sanrafaelae*



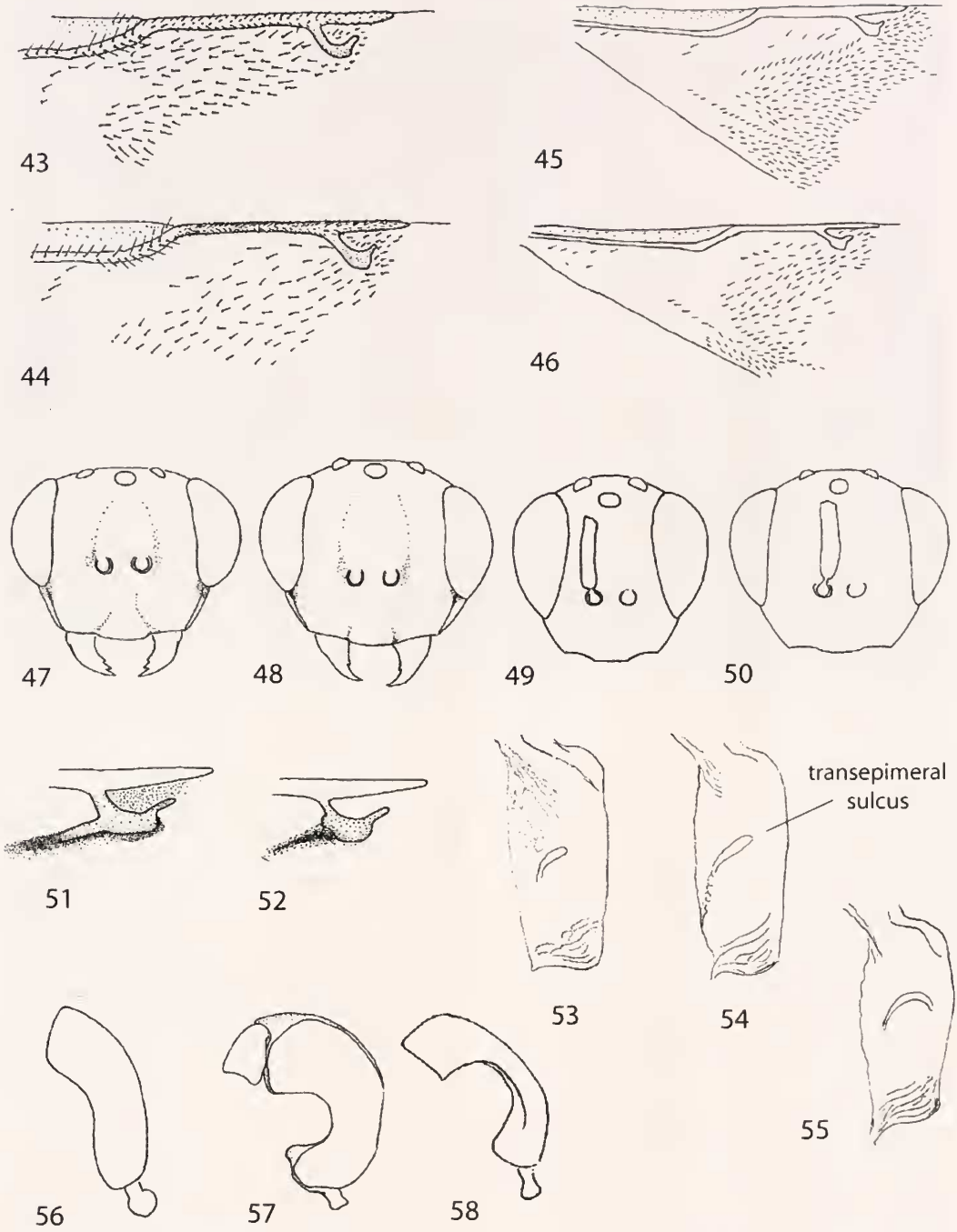
Figs. 1–11. Torymidae. 1–2, Mesosoma, side (arrow indicates anterior margin of metapleuron). 3–4, Metacoxa, side. 5–6, Propodeum, dorsal. 7–8, Mesosoma, dorsal (arrow indicates frenum). 9, Fore wing, dorsal (*Echthrodape africana*). 10, Fore wing, dorsal, showing venation terminology. 11, Head, anterior, showing measurements.



Figs. 12–28. Torymidae. 12–13, Fore wing venation, dorsal. 14–15, Head, anterior, lines indicate malar and intermalar distances. 12, 14 *Echthrodape papuana*. 13, 15 *Echthrodape africana*. 16–18, Head, posterior (showing carinae). 16, *Microdontomerus*. 17, *Pseudotorymus*. 18, *Monodontomerus*. 19–20, Antenna, side. 19, *Monodontomerus thorpi*. 20, *Monodontomerus* spp. 21–28, Head. 21–22, *Monodontomerus osmiae* (from Kamijo 1963). 23–24, *Monodontomerus anthidiorum*. 25–26, *Monodontomerus mexicanus*. 27–28, *Monodontomerus bakeri*.



Figs. 29–42. Torymidae, *Monodontomerus* spp. (except 34, *Pseudotorymus*). 29–31, Fore wing. 29, *M. aeneus*. 30, *M.* sp. 31, *M. clementi*. 32–33, Metasomal tergum 6. 32, *M. argentinus*. 33, *M. rugulosus*. 34–35, Hind femur and tibia, side. 34, *P.* sp. 35, *M. aeneus*. 36–38, Hind femur. 36, *M. thorpi*. 37, *M. argentinus*. 38, *M. rugulosus*. 39–40, Fore leg (left side view, right ventral view). 39, *M. aeneus*. 40, *M. brevicrus*. 41–42, Frenum (apex of scutellum). 41, *M. acrostigmus*. 42, *M. aeneus*.



Figs. 43–58. Torymidae, *Monodontomerus* (*Mo.*) and *Microdontomerus* (*Mi.*). 43–46, Fore wing, part. 43, *Mo. mandibularis*. 44, *Mo. parkeri*. 45, *Mi. parkeri*. 46, *Mi. enigma*. 47–50, Heads. 47, *Mo. montivagus*. 48, *Mo. mandibularis*. 49, *Mi. anthidii*. 50, *Mi. apianus*. 51–52, *M. acrostigmus* (variation in stigma). 53–55, Mesopleuron. 53, *Mo. clementi*. 54, *Mo. parkeri*. 55, *Mo. montivagus*. 56–58, Scape, male. 56, *Mo. montivagus*. 57, *Mo. mandibularis*. 58, *Mo. tepedinoi*.